THE EFFECTS OF THE EXPERIMENTAL REMOVAL OF GREEN SEA URCHINS, AND OF ICE-SCOUR ON SUBLITTORAL BENTHIC MACRO-ALGAL COMMUNITIES IN EASTERN NEWFOUNDLAND

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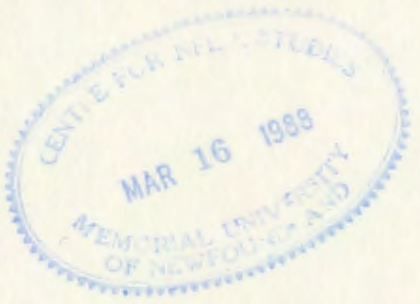

The effects of the experimental removal of green sea urchins, and of ice-scour on sublittoral benthic macro-algal communities in eastern Newfoundland

By

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Abstract

The results of an urchin removal experiment which was conducted over a four year period at a site in Conception Bay, Newfoundland are reported. The experiment was carried out to determine how the benthic algal community at a heavily grazed sublittoral Newfoundland site, subjected to periodic ice scour, would respond to a reduction in grazing pressure. Three transects were selected: one from which urchins were removed manually; one from which urchins were removed using quicklime, and one as a control. Sampling was conducted within each of three depth ranges: 0-2m, the shallow macro-algal zone; 2-3m, the upper portion of the urchin dominated zone; and 6-9m, the middle portion of the urchin dominated zone. The occurrence of ice-scour during two out of four years of the study allowed an assessment of its effects on biomass, diversity, and species composition of the algal community.

In the shallow zone (0-2m) urchins had no detectable effect on macroalgal biomass. Biomass, species composition and diversity were affected, however, by the occurrence and timing of ice-scour. In the absence of ice-scour, *Alaria esculenta* formed a canopy which shaded the substratum; few species coexisted, and diversity was low. Winter and spring ice scour, which was temporally and spatially patchy, removed the *Alaria* canopy and made available well lighted rocky substratum for colonization. Scoured patches were colonized by annual algae, resulting in an increase in diversity. Biomass returned to pre-scour levels approximately 2 mo after scouring, but diversity remained high due to the persistence of several species of annual algae in patches among the unscoured *Alaria*.

In the urchin dominated zone macro-algal biomass increased following

urchin removal by both manual and quicklime techniques. The upper portion of the resulting communities became dominated by *Alaria esculenta*, with very few co-existing species. This dominance by *Alaria* was also typical of the shallow zone in years during which no ice-scour occurred. Below the zone of *Alaria* domination (2-3m) the community became dominated by *Desmarestia aculeata*, with many other co-existent species (including *Agarum cribrosum, Alaria esculenta*, and *Laminaria digitata*).

Algal biomass in the control area was generally low, except during the summer of 1982, when an increase in both biomass and species richness occurred. The species composition, however, differed from that on the removal transects in that the control area was dominated by annual algae such as *Acrothrix novae-angliae, Chordaria flagelliformis, Dictyosiphon foeniculaceus, Ectocarpus siliculosus*, and *Eudesme virescens*. *Alaria* and *Desmarestia aculeata* were unimportant in this association because the algae recruited in the late spring and early summer, after the period of *Alaria* and *Desmarestia* recruitment.

Urchin biomass in the control area was greatest at 2-3m. Density was greatest in the middle of the urchin dominated zone (6-9m), where numerous juveniles occurred in crevices, and among branched and undercut encrusting coralline algae.

In addition to urchins, the herbivore guild in the study area consisted of six species of molluscs (*Acmaea testudinalis, Lacuna vincta, Margarites helicinus, Ischnochiton alba, Tonicella marmorea*, and *T. rubra*). Densities of *Acmaea* and the three chitons were greatest at 6-9m. Recruitment and density of the latter three species showed no detectable relationship with urchin removal. Recruitment of the annual *Lacuna* and *Margarites* occurred during the early autumn, in shallow water, particularly in the presence of macro-algae. Survival into the following spring was greatest on the macro-algae in the urchin removal areas.

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INTRODUCTION

1. The geographical perspective

Extensive rocky subtidal areas, which are devoid of large fleshy macrophytes as a result of grazing by green sea urchins (*Strongylocentrotus droebachiensis*), occur from Massachusetts to Labrador (Breen and Mann 1976, Chapman 1981, Harris 1981, Himmelman 1985, Himmelman *et al.* 1983a, Hooper 1980, Mann 1977, pers. obs. 1977-1985). Areas dominated by green sea urchins have also been reported in Europe; they occur in Norway (Hagen 1983) and on the Barents Sea coast of the Soviet Union (Propp 1977). This species has also been shown to limit algal biomass on a local scale in the eastern Pacific (Vadas 1969, Foreman 1977). Such urchin dominated communities[1] have been referred to as "barrens" (Lawrence 1975), a term used here to refer to the absence of very large, canopy-forming macrophytes such as *Laminaria*. The removal of urchins from such barren areas generally leads to the recovery of abundant macrophytes (Chapman 1981, Duggins 1980, Himmelman *et al.* 1983a, Lawrence 1975, Miller 1985).

In the north Atlantic Ocean the history of sea urchin grazing, and the factors regulating sea urchin populations in areas directly influenced by cold water [eg. north of the North Cape of Norway in Europe, Newfoundland and north in North America], may be very different than in more southerly areas influenced by warmer water (see below). Outbreaks of the green sea urchin are recent events (with in the last 16 y) in the warmer part of its range on both sides of the North Atlantic (Mann 1977, Hagen 1983), although there is evidence that

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[1]The word **community**, as employed here, refers to a group of organisms occurring in a particular environment, presumably interacting with each other and with the environment, and seperable by means of ecological survey from other such groups (Mills 1969).

such outbreaks have occurred before (Miller 1985). The urchin outbreak, which destroyed most of the *Laminaria*-dominated kelp beds off the Atlantic coast of Nova Scotia during the early 1970's (Mann 1977, Wharton 1980), was terminated by a disease caused by a parasitic amoeba (Jones *et al.* 1985, Miller 1985, Scheibling 1985). There is evidence that the outbreak which occurred in Norway will be terminated by a parasitic nematode (Hagen 1983, 1985, in press).

The situation described above contrasts with the more long-term nature of sea urchin barrens in the colder regions of both sides of the Atlantic. Sea urchin dominated barrens have predominated in the subtidal of eastern Newfoundland for at least 22 years (D.H. Steele,[2] pers. com.), and probably for much longer (Hooper 1980). There is also evidence that the barrens in the Passamaquoddy Bay area of the Bay of Fundy and in the lower St. Lawrence Estuary (both areas experience colder summer sea surface temperatures than the Atlantic coast of Nova Scotia) have existed for a much longer time than the barrens in Nova Scotia (Dawson 1867, Ganong 1885,1888, Scott 1902, Stimson 1854, Verrill 1874). Green sea urchin dominated barrens in the colder area of Europe have probably also existed for a longer time than they have in the more southerly, warmer area (Hagen 1983, Propp 1977). There is no documented case of the natural termination of green sea urchin outbreaks in the colder part of the species' range [Bay of Fundy (pers. obs. 1985), Newfoundland (pers. obs. 1977-1985), Murmansk Coast in Europe (Propp 1977)].

There have been differences in the response of the algal community to a reduction in urchin grazing, in the two regions of the northwest Atlantic where this phenomenon has been studied (Nova Scotia and the lower St. Lawrence Estuary). These differences may be related, in part, to the different history of sea urchin grazing (ie. recent *versus* more long-term). In Nova Scotia, manual urchin removal from a grazed patch within a kelp bed, as well as from a barren area 8 y after kelp bed destruction, was followed by a return of kelps, mainly *Laminaria*

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longicruris (Breen and Mann 1976, Chapman 1981). Kelp beds dominated by *Laminaria longicruris* regenerated along the Nova Scotian coast after disease-induced mass mortality of urchins (Moore and Miller 1983, Scheibling 1984, Miller 1985). In the lower St. Lawrence estuary, however, two years after the experimental removal of urchins, *Alaria esculenta* dominated in shallow water, and *Agarum cribrosum* was the most abundant species in deeper water. In contrast to the Nova Scotia situation, domination by *Laminaria longicruris* did not occur (Himmelman *et al.* 1983a).

The pattern of macro-algal distribution at urchin dominated sites in eastern Newfoundland (South 1983) differ markedly from both Nova Scotia (Breen and Mann 1976) and the St. Lawrence estuary (Himmelman 1980; Himmelman *et al.* 1983a). A shallow water refuge from urchin grazing exists in eastern Newfoundland (Himmelman 1985), and Nova Scotia (Chapman 1981). This zone was lacking in the area of the St. Lawrence Estuary studied by Himmelman *et al.* (1983a), although such a zone does occur in many areas of the lower St. Lawrence Estuary (Himmelman and Lavergne 1985). The kelp *Laminaria longicruris* is common in the shallow water refuge in Nova Scotia (Chapman 1981, pers. obs. 1980), whereas it is lacking from this refuge in eastern Newfoundland (pers. obs. 1977-1985). Himmelman and Lavergne (1985) did not state which species of *Laminaria* occurs in this refuge on the north shore in some parts of the lower St. Lawrence Estuary, but *L. longicruris* was common in the middle Estuary and on the south shore of the lower Estuary.

A second important difference among areas concerns the presence of sea ice, which occurs in the St. Lawrence Estuary (Archambault and Bourget 1983) and Newfoundland (Hooper 1980), but does not occur in that region of the Nova Scotian coast where algae-sea urchin interactions have been studied (Markham 1980). Scouring by sea ice has a major impact on benthic communities (Hooper 1980), but this was not examined in the study by Himmelman *et al.* (1983a).

Eastern Newfoundland is influenced by cold water from the Labrador

Current. In addition to the effects on the water temperature regime, the Labrador Current brings sea ice into the region, which lies south of the maximum extent of *in situ* generated winter pack ice (Dinsmore 1972). When ice drifts south with the Labrador current, onshore winds may blow the ice onshore and bring about extensive scouring of the littoral and upper sublittoral (Hooper 1981). Although it is known that ice-scour influences the ecology of algae at high latitudes (Sundene 1953; Taylor 1957; Lund 1959; Wilce 1959; Ellis and Wilce 1961; Stephenson and Stephenson 1972; Hooper 1981; Bolton 1983), there are few detailed accounts of its effects on macro-algal communities.

As a result of the physical and biotic differences among areas, including differences in the history of urchin grazing, it is impossible to generalize from one region to another in the northwest Atlantic, how barren areas respond to a natural (eg. disease) or artificial (eg. manual removal) release from urchin grazing. No study of the algal community response to urchin removal from a barren area has yet been conducted in an area influenced directly by cold Arctic water and ice-scour. None of the studies conducted in the Northwest Atlantic have examined, in detail, the changes in algal biomass, species composition, or diversity in relation to a reduction in urchin grazing at a barren site, with the exception of the study by Himmelman *et al.* (1983a).

The approach taken here is to use the well established technique of urchin removal to examine the response of the benthic algal community to a reduction in urchin grazing pressure at a barren site under the direct Arctic influence of the cold Labrador Current and ice-scour. During the present study ice-scour occurred in the research area in two of four years, permitting its effects on benthic sublittoral macrophytes to be studied concurrently with experimental urchin removal.

2. The research program

Aspects of community structure include species composition, species diversity, the relative abundances of species, the spatial and temporal patterns of species abundances, and morphological characters of the dominant species (Tilman 1982). All of these characteristics of a community may be influenced by interactions with the physical and biotic environment. I have therefore examined biomass, species composition, diversity (a combination of the number of species and the relative distribution of biomass among them), species richness, and some of the life history characters of the species which occur in the study area, in relation to the experimental reduction in sea urchin grazing, and in relation to ice disturbance. I also examined the biomass and density of the members of the molluscan herbivore guild, because grazing by other herbivores may be an important consideration in evaluating the response of macro-algae to urchin removal (*cf.* Fralick *et al.* 1974). Also, other herbivores may increase in abundance, and therefore grazing capacity, in response to an increase in algal abundance (Himmelman *et al.* 1983a).

The experimental reduction in benthic marine herbivore densities has generally involved one or more of: (1) manual removal, (2) the application of high-calcium quicklime, and (3) caging (North and Shaefer 1963; Connell 1972; Lawrence 1975). Although an exclusion net was placed around the transect from which urchins were removed, cage experiments *per se* were not employed during the present study because of the difficulties of working with cages at exposed sites. The manual-removal and quicklime methods of reducing urchin grazing were used, because they have given good results in other studies (Jones 1948; Kitching and Ebling 1961; North and Shaefer 1963; Leighton *et al.* 1966; Jones and Kain 1967; Paine and Vadas 1969; Lawrence 1975; Breen and Mann 1976; Vance 1979; Duggins 1980; Chapman 1981; Bernstein and Welsford 1982; Sammarco 1982a,b; Himmelman *et al.* 1983a).

Three subtidal transects were utilized; one left untreated as a control, one from which urchins were removed manually, and one from which urchins were

removed by quicklime application. The study sites were in Conception Bay, the outer portion of which preliminary observations showed has a species composition and zonation typical of the open Atlantic coast of Newfoundland (Himmelman 1985, South 1983).

There are generally three distinct seaweed zones on the open Atlantic coast of Newfoundland. The shallowest zone (*ca* 0-2m below mean low tide) has abundant macrophytes, which exist mainly because wave action reduces urchin foraging ability (Himmelman 1985). Preliminary observations in the study area suggested that biomass, species composition and diversity in this shallow zone is strongly influenced by ice-scour. Next is the barren zone (*ca* 2-12m below MLT) with numerous green sea urchins, and very few large fleshy macrophytes (Himmelman 1985). Below the barrens there is usually another zone with a relatively high seaweed biomass and cover, dominated by *Agarum cribrosum* and *Ptilota serrata* (Keats *et al.* 1982).

With the exception of the *Agarum/Ptilota* zone (Keats *et al.* 1982) there are no published data on macro-algal biomass and its variation among species with depth and time in the Newfoundland sublittoral. The present study was conducted between mean low water and a depth of 9m. Over a four year period detailed analyses were conducted within three separate depth ranges corresponding to distinct habitats: the shallow macro-algae dominated zone (0-2m); the upper fringe of the urchin dominated zone (2-3m); and the mid-portion of the urchin dominated zone (6-9m). Some data from the *Agarum/Ptilota* zone (12-18m), gathered during another study (Keats *et al.* 1982), are included for comparative purposes.

The research program was designed to answer the following questions: (1). What changes in macro-algal biomass, diversity, and species composition occur following the removal of urchins, and how do these changes compare with natural changes (if any) which occur in a control area over the same time period? (2). How do these changes compare with the results of studies elsewhere, particularly

in the northwest Atlantic? (3). Are there changes in the abundance of other herbivores with depth, time, or when the macro-algae are released from urchin grazing pressure? (4). How does ice-scour influence macro-algal biomass, diversity, and species composition? (5). What are the predominant life history adaptations of the algal species to grazing and ice-scour?

3. Theoretical considerations

The theoretical and conceptual framework for the questions which will be addressed in this thesis comes from studies of the effects of physical disturbance[3] (eg. ice-scour) and herbivory (eg. sea urchin grazing) on community structure.

Disturbance and herbivory have a number of parallels in terms of how they impact ecological communities. The highest diversity in a community has been predicted at intermediate levels of disturbance (Connell 1978, Levin and Paine 1974) and herbivory (Paine and Vadas 1969, see following). With no disturbance (or herbivory), dominance of a resource by a small number of competitively superior species is predicted. At high levels of disturbance (or herbivory) all species are eliminated, or a few ephemeral or species with defenses occur. Diversity is highest at intermediate levels of these factors because there are many patches of habitat at different successional stages and, therefore, different species composition (Connell 1978, Sousa 1984).

The term "level of disturbance" (or herbivory) incorporates several aspects of the disturbance regime: patch size, patch shape, the frequency of patch initiation, the intensity (physical) of disturbance, the severity (biological damage) of disturbance, predictability, and turnover rate (time required to disturb a given

---

[3]There are two competing definitions of "disturbance." One view holds that disturbance is an irregular event that moves a community away from equilibrium conditions (see White 1979). The alternative view, the one employed in most of the recent literature, and the meaning used here, is that disturbance is "a discrete, punctuated killing, displacement or damaging of one or more individuals or colonies that directly or indirectly creates an opportunity for new individuals (or colonies) to become established" (Sousa 1984). This definition makes no assumptions about the equilibrium status of the community, and it permits the study of disturbance as one of the **normal** factors influencing the community.

area under consideration) (Miller 1982, Paine and Levin 1981, Sousa 1984). In addition to the level of disturbance, the timing of disturbance (or herbivory) relative to the reproductive phenology of potential colonizers is an important consideration (Sousa 1984).

A significant feature by which herbivory differs from physical disturbance is that the relationship between level of herbivory and diversity may be modified by the preferences and foraging strategies of the members of the herbivore guild (Gaines 1985, Lubchenco and Gaines 1981). If a competitive dominant(s) is preferred then diversity is maximized at an intermediate level of herbivory, but if a competitive subordinate is preferred then diversity will decrease monotonically (Lubchenco 1978), or will show little change with increasing herbivory. Even so, a parallel with food preference may exist for disturbance, in that some species will be more susceptible than others to a particular disturbance agent (White 1979).

A second parallel exists between these factors in that disturbed patches (between disturbances) and grazed patches (released from grazing) tend to be colonized by early successional[4] species. It has been suggested on theoretical grounds and backed up by the results of some empirical studies that early successional species are selected to have life history and morphological characters adapted to the rapid colonization of available habitats (Littler and Littler 1980). These early successional species tend to be ephemerals (short lived, many generations per year), annuals (live less than one year, but only one generation per year), or perennials (live more than one year) with vegetative short-cuts (asexual reproduction with dispersal) in the life history (Littler and Littler 1980). In contrast, late-successional species tend to be predominately perennials without vegetative short-cuts. Early successional species also tend to be less structurally complex, and show higher growth rates and productivity than later successional species (Littler and Littler 1980, Steneck and Wattling 1982).

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[4]**Succession** as used here refers to the changes in a community which take place with time following a purturbation, irrespective of the mechanisms [*sensu* Connell and Slayter (1977)] involved in those changes.

If these theories are applicable to this environment, then they suggest some predictions concerning the response of the algal community to urchin removal and to ice-scour. Diversity and species richness should be higher during the early stages, than they are during the later stages following urchin removal. If ice scour is patchy and incomplete (as preliminary observations suggest that it usually is in this region) then diversity and species richness should be higher in years during which ice-scour occurs than it is in years without ice-scour. Species which colonize early after urchin removal, after ice-scour, or in temporary patches in the grazed (control) area should (on average) possess the life history characteristics attributed to early successional species (see above). Species which are more abundant in the later stages following urchin removal, and in years without ice-scour should (on average) possess the life history characteristics attributed to late successional species.

These theoretical considerations and predictions aside, I wish to emphasize that the major purpose of this thesis is to increase our understanding of geographical variation in the rôle of grazing by the green sea urchin in shallow-water, rocky bottom marine communities, the response of communities to a reduction in such grazing, and how this is influenced by the interactions with the physical environment (eg. ice-scour).

MATERIALS AND METHODS

1. Selection of sites

The locations for the three transect sites (Figure 1) were selected on the basis of the following characteristics: (1) They were representative of the open Atlantic Coast of Newfoundland (Hooper *et al.* 1980), in particular possessing urchin/coralline dominated areas, (2) They were similar in terms of slope, aspect, substratum type, and biotic communities, (3) They were steep enough in slope to allow access to a range of depths over a short distance, and (4) They were easily accessible from St. John's. On the basis of criteria 3 and 4 the area of coast between Portugal Cove and Bauline in Conception Bay was selected (Figure 1). During March-April, 1979 the area was surveyed, and the two sites were chosen on the basis of criteria 1-4 (above). A third site, to be treated with quicklime, was chosen on the same basis during May 1981. The areas were marked by weighted transect lines scaled at 2m intervals, and extending from above high water to a depth of 30m below mean low water. The study sites are hereafter referred to as control, experimental (=manual removal), and quicklimed transects.

2. Description of the study area

Subtidal macro-algae are distributed in three distinct zones (Figure 2). In the immediate subtidal there is a zone (0-2m) with abundant fleshy macrophytes. Below that there is a zone (2-12m) dominated by *Strongylocentrotus droebachiensis*, with a much reduced abundance of fleshy macro-algae. There is also a deeper zone (>12m) where *Agarum cribrosum* and *Ptilota serrata* are abundant. Coralline algae, mainly *Clathromorphum circumscriptum, Corallina officinalis, Phymatolithon rugulosum, Phymatolithon laevigatum,* and *Lithothamnion glaciale* are well developed in the study area, and cover nearly

100% of the substratum from *ca* 6m to beyond diving depths. Thickness of the corallines (*Clathromorphum circumscriptum* and *Lithothamnion glaciale*) is greatest (up to 6 cm) in the deeper portion of the barrens, and in the *Agarum/Ptilota* zone.

The 100m depth contour is approximately 200m offshore, and because of the steeply sloping bottom wave energy is dissipated on a narrow band of shore. The substratum consists of bedrock of volcanic origin from the intertidal to approximately 6m depth, and a mixture of bedrock and small densely-packed boulders to approximately 25m depth. Large (>3m diameter) boulders also occur in the area, but were avoided in the placement of the transects.

Sea surface temperatures in the vicinity of the study site range from a minimum of -1.8°C in winter to a maximum of 16°C in summer, although the annual range shows some variation (Steele 1975). Frequent temperature fluctuations occur during the spring warm-up period, due to the instability of the water column. Short-term temperature stability gradually increases with increasing thermal energy content of the water column. After September a steady decline in temperature occurs (Steele 1975).

There is little salinity fluctuation in the study area. Petrie (1980) reported a mean annual variation in surface salinity of 1 $^{o}/_{oo}$ (from 31 to 32 $^{o}/_{oo}$) off Cape Spear over the period the 1950-1959. Sandeman (1982) reported variation in the surface salinity from 31 $^{o}/_{oo}$ to 33 $^{o}/_{oo}$ over a period of 1y at a site in the inner part of Conception Bay. Mass mortality of urchins due to salinity reductions resulting from heavy spring run-off (Hooper 1980) therefore do not occur at an open site such as the present study area.

Sandeman (1982) reported variations over a 15 mo period in the concentrations of selected nutrients at a site 7 km from the present study area. From July to September nitrogen (nitrate and nitrite) concentration within the 0-10m depth range was *ca* 0.4 μg-at. l^{-1}. Nitrogen concentration rose during January (*ca* 2.5 μg-at. l^{-1}), peaked during March (5.0 μg-at. l^{-1}), declined to *ca*

0.4 μg-at. l^{-1} by mid June, and remained low throughout the summer. Phosphorous concentration was highest (*ca* 0.4 μg-at. l^{-1}) between late July and early November, and lowest in the January to March period (ca. 0.05 μg-at. l^{-1}). The mean tide range for the study area is 0.9 m (Fisheries and Oceans Canada 1983) which, combined with the steeply sloping shore, produces a narrow intertidal zone.

Wind patterns vary both seasonally, and annually (Banfield 1983). Figure 3, compiled from data in Anon. (1982), shows the mean monthly frequency of wind in 5 categories ranging from 0 (calm) through 1 (offshore), to 4 (fully onshore). Both the frequency of onshore winds and the mean speed are at their annual low in summer, increase in October, and peak during December to March. Sea states are therefore relatively calm during the summer, and highest during the autumn and winter when the study area is frequently exposed to the full force of strong onshore winds.

3. Removal of Urchins

3.1. Manual Removal

During May, 1979 (Table 1), the transect areas were marked off 5 m on either side of the transect line to a depth of 10m, over a horizontal (offshore) distance of 40 m. The marked area (400 m^2) was divided into 5 m^2 grids, and urchins were systematically killed in each grid. Removal was begun in mid-June of 1980 in the grids at 10m, and continued up the slope such that the 0-2m area was the last to have urchins removed, and this did not take place until mid-August. Urchins were smashed with hammers, and all those visible were killed. Urchins smaller than 10-15 mm test diameter occupy cryptic microhabitats, and hence were not as effectively removed as larger individuals. After the initial removal urchins were killed every 1-2 wks in summer, *ca* monthly in winter. The removal area was surrounded by a 1.5 m high fence constructed of 3 cm mesh size seine netting. The fence had a 1.5 m skirt onto which boulders were placed to seal it against the bottom.

3.2. Application of quicklime.

A preliminary surface application of 0.8 kg m^{-2} to a 10m x 10m test area, during June of 1981, eliminated a large enough portion of the urchin population to allow macro-algal colonization. An area 90 m (parallel to the shore) by 40 m (perpendicular to the shore), extending to a depth of 15 m was then marked off using lead core line at Blast Hole Bight, Conception Bay (Figure 1). The quicklime site was 0.8 km. south of the control transect.

On October 22, 1981, 1400 kg of granular high calcium quicklime (Pfizer Chemical, Adams Massachussetts) was applied using an agricultural seed spreader (Figure 4). Waves prevented the boat from maneuvering near to shore, and depths shallower than 3 m received very little quicklime. Inspection by divers 2h later revealed a patchy distribution of quicklime. Less than 50% of the substratum had received adequate quicklime. Other areas received considerably more than the 0.8 kg m^{-2} average.

Weather conditions did not permit the application of the remaining 1300 kg quicklime until November 18, when high waves again prevented an even application. Rough weather prevented further access to the site until December 5, 1981, when observations indicated that in the southern portion of the area *ca* 90% of the substratum received relatively even coverage of quicklime, with the evenness of coverage decreasing considerably toward the north portion of the area. Subsequent observations and biomass sampling were therefore restricted to the southern-most 40m (1600 m^2) of the quicklimed area.

4. Sampling Procedure

4.1. Quantitative samples

Sampling was conducted in the shallow algal zone (0-2m below mean low tide), just below that zone (2-3m) at the upper edge of the urchin/coralline zone, and well within the urchin/coralline zone (6-9m). Quadrats were constructed of 6.5mm diameter steel rods. One side was removed, and the quadrat was painted reflective yellow for ease of working within the macro-algae. During May, 1979 four preliminary samples were obtained with a quadrat area of 0.25 m^2, a size used successfully in similar habitats elsewhere (Mann 1972; Ebert 1977; Foreman 1977; Pearse and Hines 1979; Bernstein *et al.* 1981; Chapman 1981; Choat and Schiel 1982; Himmelman *et al.* 1982). Sorting and measurement logistics, however, dictated that quadrat size be reduced to 0.1 m^2, which also has been used in similar sampling studies (Paine and Vadas 1969; Lang and Mann 1976). A 0.04 m^2 quadrat was used to sample *Lacuna vincta* and *Margarites helicinus* during the autumn of 1980, after a heavy settlement yielded too many individuals to sort them from 0.1 m^2 quadrats.

A sample size of 5 quadrats per treatment was chosen initially, as plots of running means (Kershaw 1973) showed this to be an adequate number for total macro-algal and urchin biomass. Biomass of individual algal species showed greater variability than the total biomass of all algae. Sample size was therefore increased (to a maximum of 10) when logistic constraints permitted.

Table 2 shows the periods when sampling was conducted, the transect and depth ranges sampled, and the number of samples obtained. Sample periods were chosen to reflect the seasonal changes in floristics, which have been reported for the Newfoundland inshore (Hooper *et al.* 1980). These were spring (May), summer (July), and autumn (October). Rough sea conditions, and lack of adequate diving support reduced the effectiveness of sampling during the autumn, and prevented winter sampling.

Quadrats were placed by blind casting at each depth range. Material which could be harvested by hand was placed into 0.5 mm mesh collecting bags. The remaining material was then scraped from the rock surface using a combination of paint scrapers, diving knives, and hard-bristle tooth brushes. The scraped material was collected using an air dredge (Figure 5) fitted with a 0.5mm (mesh size) collecting tube.

Until the autumn of 1980 the percentage cover of individual crustose coralline species was estimated visually in quadrats prior to destructive sampling. This was discontinued because it consumed too much underwater time, but the data obtained up until that date were used to determine the distribution of coralline algae with depth.

Variables measured included total macro-algal biomass (except for crustose species), and biomass of individual species. Only species which were large enough to observe in the field, or present in large enough quantities to be seen in a sorting tray are included for analysis. Species present, but at a biomass below the resolution of the balance (0.05 g) are recorded as "present" (+). Density and biomass of the members of the herbivore guild were also determined, and the size structure of the urchin populations was studied in detail. Samples of algae and herbivores from the *Agarum/Ptilota* zone (12-18m), gathered during another study (Keats *et al.* 1982), were also used for comparative purposes.

4.2. Field observations

In addition to the destructive, quantitative samples, observations were made in the study areas as often as conditions permitted. The study area was traversed for 20-30 min within each depth range; notes on the abundance [4=dominant (>50% of biomass), 3=high biomass but patchy, not dominant, 2=small abundant plants, 1=small patchily distributed plants] of macrophyte species were recorded on plastic paper. This, when supplemented with detailed post-dive notes, and photographs of the study area, allowed the rapid collection of information when quantititive biomass samples could not be obtained. Notes were

also kept on the occurrence of sea ice in the research area. Light measurements (in F-stop units) were made on June 7, 1982 using a Sekonic Marine photographic light meter, and were converted to the percentage of the illumination at the canopy surface which reached the understorey. Only preliminary measurements were made because the light meter malfunctioned after the first day of use, so detailed light measurements are not presented.

5. Sorting, Identification, Weighing and Measuring

Laboratory sorting and identification were made on fresh or frozen material. Algae and invertebrates were sorted into species, or higher taxa, blotted for *ca* 5 min to remove surface water and wet weighed. Values obtained were converted to g (fresh wt) m^{-2} for analysis. Linear dimensions were measured using Helios calipers, accurate to 0.05 mm.

All algal species names and authorities are as per South (1984), except *Scagelia pylaisaei* (Mont.) Wynne (Wynne 1985). Invertebrate names are as per Gosner (1971) and Abbott (1974).

6. Data Analysis

Table 2 is a summary of the sampling undertaken during the study. Examination of scatter plots of standard deviations *versus* means of biomass, and frequency plots where appropriate, showed considerable heteroscedasticity and deviation from normality. Log_{10} transformations of biomass data were therefore performed prior to calculating standard errors, and a re-examination of the data showed that the transformations were effective. For graphical representation the means were converted to geometric means (Sokal and Rohlf 1969). Arithmetic means were also computed, and are presented here for comparison with published data using arithmetic means. Arithmetic means were used for calculation of percent biomass by species, as statistical tests were not performed on the resulting data. Species richness as used here represents the total number of species present in all samples, or counted during monthly observations.

To determine how patterns of diversity and species relative abundances varied under the influence of ice-scour, and urchin removal dominance-diversity curves (Whittaker 1965, May 1981), diversity (H^*) and dominance (1-J) (Wilhm 1968) were produced using a Fortran-77 program written by the author on a Digital Equipment Corporation Vax 11/780 computer. All means and standard errors were calculated using the Statistical Analysis System (Ray 1982a,b) on an Amdahl 470/V6-II or a Digital Equipment Corporation VAX 11/780 computer, or SPSS (Nie *et al.* 1975) on a VAX 11/780.

The data were not subjected to rigorous statistical tests due to problems of pseudoreplication (Hurlbert 1984), and missing data due to the difficulties of working in this environment. In most cases means and standard errors are presented, along with field observations, and the reader can judge whether to accept biological significance from this information. This is the approach recommended by Hurlbert (1984) when it is necessary to work in environments where it is not possible to produce a true replicated and balanced experimental design.

Confidence limits about an estimate of percentage urchin biomass removed were made based on the *a priori* contrasts of untreated (i.e. control and pre-removal experimental transect samples) *versus* treated (i.e. post-removal experimental or quicklimed transect samples) for each depth range averaged over all sample periods. These confidence limits were set by:

1. Computing the 95% confidence limits about the means of the $\log_{10}$ transformed variates;
2. Transforming these to the geometric mean with confidence limits;
3. Computing the mean % biomass removed by taking:

$$\% \text{ removed} = ((X_{\text{untreated}} - X_{\text{treated}})/X_{\text{untreated}}) \times 100\%$$

4. Computing the lower confidence limits for the % biomass removed by taking:

$$LCL=((LCL_{untreated}-UCL_{treated})/LCL_{untreated})x100\%$$

and,

5. computing the upper confidence limit for the % biomass removed by taking:

$$UCL=((UCL_{untreated}-LCL_{treated})/UCL_{untreated}x100\%$$

The percentage of biomass removed from the quicklimed transect was similarly estimated by comparison with control condition samples.

The percentage survival (over the autumn-spring) of the gastropods *Lacuna vincta* and *Margarites helicinus* from the autumn of 1980 recruitment was calculated by comparing spring or summer 1981 densities with densities from the previous autumn.

Cluster analysis of algal species biomass data was carried out using CLUSTAN (Wishart 1978) implemented on a Digital Equipment Corporation Vax 11/780 computer. The similarity matrix was generated using Euclidean distance, with clustering by group average sorting (Wishart 1978). Sample sets were clustered on the basis of $\log_{10}$ mean biomass. Species recorded only as present (i.e. too little to weigh), or which occurred in less than two samples overall were excluded from the analysis. Certain other species were grouped at the generic level (see Table 3) because of uncertainty of the accuracy of identification during the early part of the study (*Giffordia*, *Ectocarpus*, *Desmarestia*).

To determine how species richness and biomass were divided among annual and ephemeral *versus* perennial algae (*sensu* Feldmann 1966) the number of species and biomass of both[5] was computed for the following conditions: (1) 0-2m

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[5] **annual** and **ephemeral** are considered together on theoretical grounds (see page 8), and because the distinction is not always possible to make. All reference to **annual** in figures therefore includes annuals and ephemerals in the **annual** category

during years in which ice-scouring occurred, (2) 0-2m during years in which no ice-scouring occurred, (3) 2-3m contrcl conditions (i.e. control and pre-treatment experimental transect), (4) 6-9m control conditions, (5) 2-3m experimental transect 2 mo after urchin removal, (6) 6-9m experimental transect 2 mo after urchin removal, (7) 2-3m removal areas (i.e. experimental and quicklimed transects), more than 9 mo after urchin removal, and (8) 6-9m removal areas more than 9 mo after urchin removal. The assignment of an alga to annual or perennial status (Table 3) was based on information from Taylor (1957) and South and Hooper (1980). The number of species of annuals and perennials was computed both with, and without species whose mean biomass was less than the accuracy (0.05 g) of our weighing balance (i.e. those recorded only as "present") included.

To determine if the increase in macro-algal biomass and species richness which occurred in the control area during the summer of 1982 was confined to the immediate area, or if these algae were also abundant at other localities, observations were made at 18 sites between Topsail Head and Cape St Francis, Conception Bay. This was done because such an increase may have been attributable to the manipulation of urchin densities in nearby areas, particularly at the quicklimed site. Each site was traversed for 20 minutes, in a direction parallel to the shore. At the end of the dive a subjective estimate was made of the percentage algal cover as the dive site, and abundant species were noted.

RESULTS

1. Description of ice scour episodes

In 1979 first-year ice[6] (*ca* 60% ice cover) drifted into Conception Bay during mid-April (Figure 6). It was present for six days, when offshore winds moved it out of the bay. Observations indicated that in the 0-2m depth range 40% of the cover of large fleshy algae had been removed by scouring, leaving well lighted substratum available for the colonization and regrowth of macro-algae. In 1980 first year ice (*ca* 60% ice cover) moved into the bay during the second week of February. Ice was present for 4 days, after which no further ice-scour occurred. Observations indicate that again 40 % of the substratum in the 0-2m depth range had been scoured. No scouring occurred in the study area subsequently. Significant ice-scour was confined to the intertidal and the upper subtidal, but in both years ice-scour was not uniformly distributed within those zones. With the exception of crevices, the intertidal and the upper 0.5 to 1 m of the subtidal was completely scoured of upright macroscopic algae; a 0.5 to 1m wide band along the lower edge of the shallow algae-zone remained unscoured; the intermediate *ca* 0.5 to 1m was patchily scoured.

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[6]Markham (1981) defines **first-year ice** as sea ice of not more than one winter's growth, with a thickness from 30 cm to 2 m. Multi-year (or "old") ice in contrast has survived at least one summer's melt, so most topographic features are smoother than on first-year ice. Multi-year ice is much harder than first-year ice (Dinsmore 1972).

2. Macro-algal abundance

2.1. Percentage cover of coralline algae with depth prior to urchin removal

Clathromorphum circumscriptum had the highest percentage cover within the 0-2m, 2-3m, and 6-9m range (Figure 7). *Corallina officinalis* was the only other coralline alga with measurable cover at 0-2m. *Corallina* reached peak cover at 2-3m on both transects, had low cover values at 6-9m, and was rare within the *Agarum/Ptilota* zone. *Lithothamnion glaciale* cover was negligible at 0-2m and increased with depth to a maximum in the *Agarum/Ptilota* zone. *Lithothamnion lemoineae* was present at 6-9m, but was rare in the study area, and did not occur in quadrat samples. *Phymatolithon laevigatum* and *P. rugulosum* had highest cover values in the 6-9m depth range. Total coralline cover was lowest at 0-2m. At 6-9m both *Clathromorphum* and *Lithothamnion* formed encrustations up to 4 cm thick. These encrustations were under-cut by boring sponges, and polychaetes. The under-cut and rugose corallines provided shelter for a variety of animals, including juvenile urchins, chitons (*Tonicella* spp.), *Hiatella arctica*), nemerteans, polychaetes, encrusting bryozoans and ascidians.

2.2. Total non-calcareous macro-algal biomass

Total fleshy macro-algal biomass at 0-2m was high throughout the study, and showed no significant change with time or between transects (Figure 8). During 1979 and 1980 biomass at 2-3m on the control transect was negligible, but it increased to 100 g m^{-2} during the summer of 1981. Biomass decreased again when the algae were removed by urchin grazing during the autumn. Biomass was negligible at 6-9m on the control transect prior to the summer of 1982, when it increased considerably at both 2-3m and 6-9m (Figure 8). On the experimental transect, at depths corresponding to the urchin dominated zone (2-3m and 6-9m), macro-algal biomass increased after urchin removal (Figure 8). At both 2-3m and 6-9m on the quicklimed transect biomass increased after treatment. During the summer of 1982, however, when an increase in biomass occurred on the control transect, there were no significant among transect differences (Figure 8).

The overall arithmetic mean biomass at 0-2m was 4412 g m^{-2} (N=57, s.e.=488), at 2-3m without urchin removal it was 249 g m^{-2} (N=43,s.e.=88), at 2-3m > 7 mo. after urchin removal it was 2999 g m^{-2} (N=37, s.e.=581), at 6-9m without urchin removal it was 114 g m^{-2} (N=49, s.e.=57) and at 6-9m after urchin removal it was 1494 g m^{-2} (N=30, s.e.=413). Biomass within the 2-3m depth range increased after urchin removal, and was nearly equal to biomass at 0-2m. Although biomass also increased at 6-9m, it was lower than biomass at the shallower depths.

2.3. Cluster analysis of macro-algal species biomass means

Figure 9 shows the results of a cluster analysis of the $\log_{10}$ mean algal biomass data for each transect, sample depth range, and sample period combination (hereafter refered to as "sample set"). Sample sets from 12-18m, within the *Agarum/Ptilota* zone (data from Keats *et al.*, 1982) are also included for comparative purposes. Four major groups are evident in the dendrogram (Figure 9). Group "A" consists of sample sets from 0-2m during years in which ice scouring occurred. The strong influence of ice-scour on community composition within the shallow algae zone is evident in the separation of this group from all other sample sets (Group "B"). Group "C" consists of sample sets from 0-2m taken during years in which ice-scour did not occur, and samples from 2-3m on the manual removal and quicklimed transects taken more than 9 mo. after urchin removal. The community which developed at 2-3m following urchin removal was thus a downward extension of the community which occurred in the 0-2m depth range in the absence of ice-scour.

Group "D" contains sample sets from the control transect at both 2-3m and 6-9m; from the manual removal transect at 2-3m prior to, and during the first autumn after urchin removal; and from both the manual removal and quicklimed transects at 6-9m before and after urchin removal. The association which developed in the 6-9m depth range after urchin removal had more in common with the association at both 2-3m and 6-9m under control conditions than with

the shallower or deeper associations. Group "E" consists of sample sets from the *Agarum/Ptilota* zone (12-18m).

2.4. Species composition at 2-3m and 6-9m

The descriptions presented here are based on algal biomass data (Figures 10-12, Figures 26-29, Appendix A) and, for time periods when quadrat samples were not taken, on presence absence data (Tables 4,5), and field notes on abundance. Where possible the situation being described is illustrated with photographs taken in the study area. The descriptive information is presented because it provides information from outside periods during which quantitative samples were obtained. This information is crucial to an understanding of the changes which took place, both in the urchin removal and control areas.

2.4.1. Species composition in the control area

Prior to the removal of urchins both the control and experimental transects had a low fleshy algal biomass and few species. *Desmarestia aculeata* and *D. viridis* were fairly common in the 2-3m depth range during all summers (Figures 11, 13, Table 4). Other species which were present, but had low biomass during the summer included *Acrothrix novae-angliae*, *Chordaria flagelliformis*, *Dictyosiphon foeniculaceus*, *Ectocarpus* spp., (*E. fasiculatus* and *E. siliculosus*), *Eudesme virescens*, *Petalonia fascia*, *Pilayella littoralis*, *Polysiphonia urceolata* and *Scytosiphon lomentaria* (Table 4, Figure 27, Appendix A). Prior to 1982, most of these summer species disappeared during the autumn, and except for *Polysiphonia flexicaulis* and *Polysiphonia urceolata* the 2-3m depth range was essentially barren throughout the autumn to early spring. In 1981 and 1982 *Urospora wormskjoldii* was observed in dense carpets on the tops of ridges following rough seas in April, but it was removed by urchin grazing during calmer sea conditions in late April and early May (Figure 14).

There was a large increase in macro-algal biomass at both 2-3m and 6-9m during the summer of 1982 (Figure 8). The species which increased were largely those present at low biomass at 2-3m during previous summers. At 2-3m

Ectocarpus siliculosus became very widespread during June, and by early July it comprised 25% of the biomass (Figures 15, 27). *Petalonia*, *Pilayella*, and *Scytosiphon* appeared in the study area, and *Scagelia pylaisaei*, *Ceramium rubrum*, and *Rhodomela confervoides* were present in small quantities. *Tilopteris mertensii* was common, but sparsely distributed within the 2-3m depth range. *Eudesme* appeared, grew rapidly to a large size, then died back, but persisted through this period. Its biomass was considerably higher than it was during previous sampling periods, and it made up 15% of the total. *Chordaria* became abundant and developed a sparse population of epiphytic *Dictyosiphon*. *Acrothrix novae-angliae* appeared during June, but was gone by late August. *Saccorhiza* juveniles were present during this period, but they were not abundant. A few *Chorda tomentosa* and *Laminaria digitata* recruited during the winter and spring, but disappeared by late July. A few scattered small *Alaria* plants were also present during this period. Both species of *Desmarestia* remained fairly common, but still very patchily distributed.

During the summer of 1982 fleshy macro-algae were abundant and fairly evenly distributed at 6-9m. Prior to 1982 this portion of the control area was essentially barren of fleshy algae. *Acrothrix*, *Chordaria*, *Eudesme*, some juvenile *Laminaria*, *Pilayella*, *Scagelia pylaisaei*, *Polysiphonia flexicaulis*, and *P. urceolata* became fairly abundant at 6-9m (Figure 29, Appendix A). *Desmarestia aculeata* and *D. viridis* were present in about the same quantities as at 2-3m. *Ectocarpus siliculosus* was the most abundant species at 6-9m during this period (30% of total biomass), although it was more patchy than at 2-3m. *Eudesme* was also a significant component of the vegetation, comprising 26% of the total biomass.

By February 1983 most of the species present during the previous summer and autumn were gone. At 2-3m only *Desmarestia aculeata*, *D. viridis*, *Petalonia*, and *Scytosiphon* remained. At 6-9m only a few new recruits of *D. aculeata* were observed, and this portion of the area had reverted to an essentially barren condition.

2.4.2. Summary of changes in algal species composition in the urchin removal areas following urchin removal at 2-3m and 6-9m

INITIAL STAGES (July-Aug, 1980)

In the early stages of urchin removal the coralline substratum throughout the study area became covered by a dense diatom turf, and a mixture of *Ectocarpus siliculosus* and *Pilayella littoralis* (Figure 16). At the same time there was an increase in survival, and perhaps recruitment, of summer annuals, especially *Acrothrix novae-angliae*, *Chordaria flagelliformis*, and *Eudesme virescens* (Figure 16b); these species were also present in low abundance at 2-3m on the control transect. Large *Desmarestia aculeata* and *Desmarestia viridis* were also present.

AUTUMN OF YEAR 1 (Sept.-Nov., 1980)

By late-September/early-October, with the exception of *Desmarestia aculeata*, most of the above taxa had disappeared. Certain Rhodophyta increased in abundance (Figure 17); these included species with perennating rhizoidal systems (*Polysiphonia urceolata* and *Scagelia pylaisaei*), as well as *Ceramium rubrum*, *Polysiphonia flexicaulis* and *Rhodomela confervoides* (Figure 26). A few *Laminaria digitata* plants colonized throughout the 2-9m depth range.

WINTER OF YEAR 1 (Dec.,1980-Mar., 1981)

Desmarestia aculeata and *D. viridis* recruitment occurred throughout the 2-9m depth range, with greatest abundance in the 6-9m portion of the area. A few *Alaria* sporelings appeared at 2-3m beginning in December, and an extremely heavy recruitment occurred during March of 1981 (Figure 18). Only a few, scattered *Alaria* sporelings appeared in the 6-9m range on the experimental

transect. *Agarum cribrosum* and *Ptilota serrata* were first observed in small quantities at 6-9m during the winter-spring of 1981 (Figure 19).

SPRING OF YEAR 1 (Apr.-May, 1981)

By April *Alaria* biomass was high (Figure 10), and it was the dominant species (76% of biomass) at 2-3m (Figure 26). A few large individuals of *Laminaria digitata*, *Desmarestia aculeata* and *Desmarestia viridis* were also observed, but their distributions were patchy (Figures 11, 12). *Monostroma grevillei* also occurred, but biomass was low (geometric mean 9 g m^{-2}). A few small plants were also observed at 6-9m. At 6-9m observations indicated that *Desmarestia aculeata* was the most abundant species, although *L. digitata* made up 49% of biomass in quadrat samples and *Desmarestia* 41% of biomass. Most of the Rhodophyta mentioned on p. 26 were still found in the understorey. Other large algae, such as *Alaria esculenta*, *Agarum cribrosum*, also co-existed with *D. aculeata* (Figure 20). In addition, a few *Saccorhiza dermatodea* sporelings appeared at both 2-3m and 6-9m during April.

SUMMER, YEAR 1-2 (JUNE-AUG., 1981)

There was little change in the community composition at 2-3m during this time. *Alaria* was the most abundant species (51% of biomass) (Fig 26). A few small *Giffordia* sp. plants were observed (also at 6-9m), but they were rare. Towards the middle of August the distal portion of the *Alaria* blades became very eroded, although no plants that were eroded below the meristematic region were observed.

At 6-9m the percentage of biomass made up by *Desmarestia aculeata* increased considerably (63%) due to the attainment of a large size by the sporophytes (Figure 28). *Laminaria digitata* and *Agarum cribrosum* were abundant (Figure 28), but they were patchily distributed (Figure 12, Appendix A). A few summer annuals (*Acrothrix novae-angliae*, *Chordaria flagelliformis*,

Dictyosiphon foeniculaceus, *Eudesme virescens*, and *Scytosiphon lomentaria*), and *Callophyllis cristata* appeared in the removal area but did not become very abundant.

AUTUMN, YEAR 2 (Sept.-Oct., 1981)

At 2-3m *Chorda tomentosa*, *Desmarestia viridis*, and *Scytosiphon lomentaria* disappeared. *Antithamnionella flocossa*, and *Ceramium rubrum* reappeared, and *Polysiphonia flexicaulis*, *P. urceolata*, and *Rhodomela confervoides* showed renewed recruitment and growth. The renewed rhodophyte growth and recruitment coincided with the period of maximum erosion of the *Alaria* canopy.

At 6-9m the annuals *Acrothrix novae-angliae*, *Chorda tomentosa*, *Eudesme virescens*, *Desmarestia viridis*, *Pilayella littoralis*, and most of the *Dictyosiphon foeniculaceus* also disappeared. Some *Dictyosiphon* remained until December, attached to the barely discernable remnants of a few decaying *Chordaria* plants. During this time there was a reappearence of *Antithamnionella floccosa* and *Ceramium rubrum*, and renewed recruitment and growth of *Scagelia pylaisaei*, *Polysiphonia flexicaulis* and *Rhodomela confervoides*. *Ceramium rubrum* and *P. flexicaulis* were most abundant as epiphytes on *Desmarestia aculeata*, but they also occurred on the substratum.

WINTER, YEAR 2 (Dec. 1981-March, 1982)

At 2-3m *Scagelia pylaisaei* and *Ceramium rubrum* attained maximum abundance, being found on the substratum under the *Alaria* and epiphytic on it. *Polysiphonia urceolata* decreased and *Pilayella littoralis* disappeared in the *Alaria* understorey. *Desmarestia aculeata* disappeared completely, presumably due to storm mortality. A few *Desmarestia viridis* germlings appeared in the area, but did not survive. Neither *D. aculeata* nor *D. viridis* were observed at 2-3m on the experimental transect after this period. The *Laminaria* population

was reduced to a few individuals in the *Alaria* understorey. A heavy recruitment of *Alaria* germlings occurred during this period in the few storm generated gaps in the canopy, and in the areas opened up due to blade erosion. When combined with the onset of rapid growth, this resulted in a rapid closure of the *Alaria* canopy. By the end of this period the few remaining *Polysiphonia flexicaulis* plants were gone, partly as a result of being eroded off with the distal ends of the rapidly growing *Alaria*.

At 6-9m *Scagelia pylaisaei*, *Antithamnionella floccosa* and *Ceramium rubrum* reached maximum abundance for the year. *Rhodomela confervoides* underwent considerable mortality during this period, but was still quite common and the remaining plants were very large (up to 30 cm in length). A few *Agarum cribrosum* sporophytes appeared and reached 20-30 cm in stature by April. Some *Alaria* recruitment at 6-9m also occurred. Juvenile *Alaria* were common near patches of mature sporophytes, which recruited during the previous winter, but were rarely observed more than 1-2m away from these patches. A few decaying *Chordaria* plants persisted throughout this period, but the epiphytic *Dictyosiphon* was not observed. The few *Saccorhiza* and *Scytosiphon* plants disappeared during this period.

SPRING, YEAR 2 (April-May, 1982)

At 2-3m on the experimental transect *Antithamnionella floccosa*, *Rhodomela confervoides*, and the few remaining *Saccorhiza* sporophytes disappeared; *Ceramium rubrum* decreased to a few very small plants. Approximately 10-15 juvenile *Chordaria* plants recruited to the area. This is the first time period during which detailed observations were made on the quicklimed transect. The species composition at 2-3m there was similar to that on the experimental transect during the spring of the previous year. The *Alaria* sporophytes, which recruited during the winter, had attained a large size and the percentage of biomass *Alaria* comprised was high (Figure 26). Some *Desmarestia aculeata* and *D. viridis* germlings appeared during this time, and had attained a

large size by May. *Laminaria digitata* germlings were present in the *Alaria* understorey, but they did not grow beyond 1-4 cm in height. *Saccorhiza* sporelings also recruited to the area and grew rapidly to 30-50 cm tall in a few patches on boulders that had evidently (as indicated by the position of the coralline cover) been overturned during a winter storm. *Urospora wormskjoldii* was very common in patches on bedrock and large boulders. The presence of battered *Alaria* holdfasts indicated that these patches were probably made available for colonization by the scouring action of moving boulders. *Urospora* was not present among the dense *Alaria* throughout most of the quicklimed site at 2-3m. A few *Giffordia* sp. plants were observed.

At 6-9m on the experimental transect *Scagelia pylaisaei*, *Antithamnionella floccosa*, *Ceramium rubrum*, and *Rhodomela confervoides* became uncommon, as they did at 2-3m. The *Agarum* plants, which recruited to the area during the winter, increased to more than 30 cm in length. A few *Chordaria* and *Saccorhiza* plants recruited to the experimental transect, but they did not become very abundant. Approximately 8-12 small *Scytosiphon* plants were observed in a single patch. Only two large (> 20 cm) *Desmarestia viridis* plants were present in the area, and no juveniles were observed. *Desmarestia viridis* began to appear on the experimental transect at 6-9m in December of 1980. *Desmarestia aculeata* appeared at the same time but was much more abundant than *D. viridis*. The *D. viridis* individuals from the 1980 colonization disappeared during the autumn of 1981, but most of the *D. aculeata* survived the winter. No further colonization by either conspecific or *D. viridis* individuals occurred. Thus *D. aculeata* comprised much of the biomass, and only two *D. viridis* plants were observed at that depth in the experimental area during 1982 (Figure 28). Although it was noted that *Desmarestia aculeata* was the most abundant species, no detailed observations were made at 6-9m in the quicklimed area during this period.

SUMMER, YEARS 2-3 (June-Aug., 1982)

On the experimental transect in early summer *Alaria* comprised most of the

algal biomass (Figure 26), and most other species were rare. Towards the end of this period at 2-3m, as the *Alaria* canopy again became very eroded, a number of species increased in abundance and some became very widespread in the understorey and epiphytically on the *Alaria*. These included *Scagelia pylaisaei*, *Ceramium rubrum*, *Polysiphonia flexicaulis*, *P. urceolata*, *Rhodomela confervoides*, and *Derbesia marina*. *Palmaria palmata* was observed for the first time at this depth on the quicklimed transect. It was epiphytic on the *Alaria* stipes, but only a few small plants were observed. The 5-6 *Chordaria* plants present attained a large stature. The species associated with erosion of the *Alaria* canopy on the experimental transect also increased in abundance on the quicklimed transect. Very small (< 5 cm) *Laminaria digitata* sporophytes were widespread in the understorey, but showed little or no sign of growth in length during this period. A few *Desmarestia aculeata* and *D. viridis* were present on the quicklimed transect, as they were on the experimental transect during the previous year. A small number of *Chorda tomentosa* plants were observed at the beginning of June, but they did not survive into July. *Chordaria* and *Eudesme* were present, but did not attain a large size or become abundant. *Ectocarpus* spp. (mainly *E. siliculosus*) became very widespread as epiphytes on *Alaria* in the quicklimed area.

At 6-9m on both the experimental and quicklimed transects there was an increase in the abundance of some of the species which increased at 2-3m (*Scagelia*, *Ceramium*, *Polysiphonia flexicaulis*, *P. urceolata*, and *Rhodomela*). At 6-9m, with the exception of *P. urceolata* these species were most abundant as epiphytes on *Desmarestia*. About 8-12 *Phycodrys rubens* plants were observed on the experimental transect, but none were seen on the quicklimed transect. No *Ptilota serrata* was observed, and *Agarum* was rare (<10 plants in the whole area) on the quicklimed transect. The *Desmarestia* canopy was much more closed than on the experimental transect. Although their distributions were extremely patchy, both *Ptilota* and *Agarum* were fairly common on the experimental transect. *Alaria* was also less abundant at 6-9m in the quicklimed area. A few *Chordaria* plants were present on both the experimental and the

quicklimed transects, but they were uncommon. *Dictyosiphon* was observed only in the quicklimed area. Although *Desmarestia aculeata* was by far the most abundant species in the quicklimed area (Figure 21), the quadrat samples did not reflect it (Figs. 11,28). The *Desmarestia* was heavily overgrown by epiphytic *Ectocarpus siliculosus* (49% of the total biomass). This estimate is probably high, but it does illustrate the importance of *Ectocarpus* at this time. *Ectocarpus siliculosus* was much less abundant in the experimental area. Large individuals of *Laminaria digitata* were fairly common, but extremely patchy on the experimental transect (Figure 22). On the quicklimed transect, however, *Laminaria* was present only as a few small (< 5 cm) individuals in the *Desmarestia* understorey. *Petalonia* and *Scytosiphon*, both rare or absent on the experimental transect, were more common (but still very patchy) on the quicklimed transect. Upright forms of these taxa were largely restricted to small boulders which had been overturned during rough weather. The crustose forms of *Petalonia* and/or *Scytosiphon* were extremely abundant in the *Desmarestia* understory of both the experimental and quicklimed transects at 6-9m.

Table 6 presents the percentage of the total biomass for each species on the control, experimental, and quicklimed transects during this period. It is evident from this that there were differences among transects in species composition, especially at 2-3m (see also page 23, and Figs. 26 to 29). These data and observations indicate that *Acrothrix*, *Chordaria*, *Desmarestia* spp., *Dictyosiphon*, *Ectocarpus siliculosus*, and *Eudesme* are important members of a summer community of macro-algae which occurs during certain years. When urchin grazing was reduced these species were excluded by extensive *Alaria* in shallow water (2-3m) and by *Desmarestia aculeata* and other canopy-forming species in deeper water (6-9m).

AUTUMN, YEAR 3 (Sept.-Oct., 1982)

Observations during this period were restricted to September and October at 2-3m, and to September at 6-9m. Few major changes took place on either the

experimental or the quicklimed transect at either of the two depth ranges during this period. The *Alaria* canopy was heavily eroded, and those species which began to increase in abundance during the late summer continued to do so at this time. *Derbesia marina* in particular became very abundant at 2-3m on the experimental transect, and virtually covered the substratum and the *Alaria* stipes. *Gloiosiphonia capillaris* was observed in the study area for the first time, and occurred at 2-3m only on the experimental and the quicklimed transects. It was fairly common, but the plants were sparsely distributed and very patchy.

WINTER, YEAR 3 (Feb., 1982)

At 2-3m on the experimental transect *Alaria* remained the most abundant species. It had begun renewed growth and the canopy was beginning to close. There was some recruitment of germlings in the understorey, but they were not abundant. The summer-autumn species, *Chordaria*, *Ectocarpus*, and *Gloiosiphonia* were gone. Juvenile *Laminaria* were present in the understorey, but no large sporophytes were observed. *Pilayella* had disappeared, and *Scagelia pylaisaei*, *Antithamnionella floccosa*, *Ceramium*, *Polysiphonia flexicaulis*, *P. urceolata*, and *Derbesia*, had declined to a few scattered plants. This situation was duplicated at 2-3m on the quicklimed transect, with a few exceptions: A few large *Desmarestia aculeata* sporophytes persisted. *Desmarestia viridis*, which had been present during September, was gone and there was no sign of new recruitment. Although juvenile *Laminaria* were more abundant in the *Alaria* understorey on the quicklimed transect, few large sporophytes were present. A small amount of *Palmaria* was observed attached to *Alaria* in the quicklimed area, but not in the experimental area.

At 6-9m on the experimental transect *Desmarestia aculeata* remained the most abundant species, but the large algae *Alaria*, *Agarum*, and *Laminaria* also persisted. Decreases in the abundance of summer-autumn species paralleled those at 2-3m. There was some new recruitment of *Desmarestia aculeata*, but *D. viridis* was not observed. On the quicklimed transect the situation was similar,

except that associated large algae were much less abundant. No *Agarum* was observed, but a few plants were probably present and overlooked due to the short observation period (*ca* 15 min). Juvenile *Laminaria* were abundant in the *Desmarestia* understorey, but no large sporophytes were observed.

OBSERVATIONS MADE AFTER FEBRUARY, 1982

In an experiment (not reported here because it was a failure) initiated during November of 1981 I transplanted six fertile *Laminaria longicruris* sporophytes into the southern side of the quicklikmed site. Within 40 days the sporophytes were consumed by a group of urchins which invaded from outside of the treated area. One large, fertile sporophyte of *L. longicruris* was observed at 9m, and two at 4m during the summer of 1984, suggesting that they appeared during the previous winter. It is not known whether these sporophytes arose from gametophytes derived from spores released by the transplanted sporophytes, or from sporophytes located some distance from the study area. Althouth it is possible that gametophytes survived for two years before producing sporophytes, the latter case seems more likely, in view of this two year time lag between the transplantation, and when the sporophytes appeared.

Although sampling was completed in 1982, I attempted to maintain the manual removal area with a low urchin grazing pressure by smashing urchins at irregular intervals until August of 1983. Large numbers of urchins began to invade the manual removal area during the autumn of 1983. By April of 1984 urchins had removed all fleshy macroalgae except for *Agarum* and *Ptilota*. As of September 1984 these plants showed no detectable sign that they were incurring mortality as a result of grazer damage, and most of the dense groups of urchins had dispersed from the area. During the autumn of 1985 a few of the *Agarum* plants were still present. This process was repeated on the quicklimed transect, but because of the larger size of the quicklimed area it took one more year for urchins to completely eliminate all algae except for *Agarum* and *Ptilota*.

2.5. Analysis of species richness trends, and species importance curves

Figure 23 shows species richness for 0-2m, based on quadrat samples because monthly species counts were not made within this depth range, and for 2-3m and 6-9m based on monthly species counts. Species richness at 0-2m decreased after 1980 on both the experimental and control transects. Figure 24 shows the species importance curves for the 0-2m biomass data, pooled by year and transect. The number of species which made up more than 0.1% of biomass was higher during 1979 and 1980. The percentage of biomass comprised by *Alaria* was greater during 1981 and 1982. Although species richness and diversity were generally greater during 1979 and 1980, there was still a tendency for most of the biomass to be made up of one or two species. *Chordaria* made up the highest percentage of biomass during 1979. A mixture of *Alaria* and *Saccorhiza* comprised the largest fraction of biomass during 1980. In 1981 and 1982 more than 90% of the biomass was *Alaria*.

At 2-3m on the control transect, a peak in species richness occurred during the spring and summer months (May-August), and during 1979, 1980, and 1981 a sharp decline in the number of species occurred during the late summer and early autumn (September-October) (Figure 23). A net increase of two species was noted during the autumn (October) of 1981, when *Polysiphonia flexicaulis, P. urceolata*, and *Rhodomela confervoides* appeared, but *Desmarestia viridis* disappeared. Species richness began to increase in January of 1982, and peaked during July. The peak persisted into the early autumn (October), and decreased again by February of 1983.

At 6-9m there were very few species of macro-algae on the control transect until the spring and summer of 1982. A peak in species richness lasted at least until September of that year, but had decreased to a single species (*Desmarestia aculeata*) by February of 1983. As occurred at 2-3m, there was an increase in species richness on the control transect during the summer of 1982.

At 2-3m the difference between control and experimental transects became

apparent during urchin removal in August of 1980. During August of 1980 the number of species on the experimental transect increased, while decreasing on the control transect. Although there was an increase in species richness on the control transect during the summer of 1981, species richness also increased on the experimental transect and it had the greater number of species. From August 1981 to June 1982 there was a steady decline in the number of species present at 2-3m on the experimental transect. Species richness on the control transect increased considerably during the spring of 1982, and from spring to early autumn the experimental transect had fewer species than the control transect. During the winter of 1982/83 the number of species present on the control transect declined considerably, while showing a smaller decrease on the experimental transect. By February of 1983 the experimental transect again had more species than the control transect.

Species richness at 2-3m in the quicklimed area followed a similar pattern to that on the control transect during April to October of 1982. During February of 1983 it was greater on the quicklimed transect than on either the experimental or the control transect. Species richness during February, 1983 was similar to that on the experimental transect in the same month of the previous year.

At 2-3m, after urchin removal, the number of species decreased as *Alaria* increased in abundance, and the *Alaria* canopy became closed (Figure 25). Light readings under the closed canopy ranged from 0-5% of levels at the canopy surface, but were usually much less than 1%. Thus 95-100% of the irradiation incident at the canopy surface was probably removed by the canopy. The erosion of the *Alaria* blades during the late summer and early autumn released a portion of the light resource. During that time an increase in the number of species (*Scagelia pylaisaei*, *Ceramium rubrum*, *Polysiphonia flexicaulis*, *P. urceolata*, and (1982 only) *Derbesia marina*) occurred (Figure 23). During the late winter of 1982 the number of species declined again as the *Alaria* canopy became closed, reducing the amount of light reaching the understorey.

Figure 26 presents the species importance curves for the 2-3m sample sets from the experimental and quicklimed transects after urchin removal. Diversity was greatest during the first autumn, two months after urchin removal. Diversity decreased with time following urchin removal, and dominance by *Alaria* increased.

Figure 27 shows the species importance curves for the control transect at 2-3m, and the experimental transect prior to urchin removal. It is evident that although biomass was greater on the experimental transect at 2-3m (Figure 8), in general, diversity was greater on the control transect than on the *Alaria* dominated experimental and quicklimed transects. Exceptions to this were those periods during which essentially no macro-algae were present on the control transect (autumn, 1979; autumn, 1980; and spring, 1982).

At 6-9m the difference between the control and experimental transects also became evident in August, during urchin removal. The experimental transect continued to have the greater number of species throughout the study, although the difference was less during the increase in macro-algal abundance which occurred during the summer of 1982. The quicklimed transect also had a greater number of species than the control transect.

Figure 28 shows the species importance curves for the 6-9m sample sets from the experimental and quicklimed transects after urchin removal. The tendency towards strong domination by a single species, although evident, was less pronounced than at 2-3m, or 0-2m in years (1981,1982) in which no ice scouring occurred. Most biomass, after the spring of 1981, was *Desmarestia*, but there were more species of intermediate relative abundance than there were at shallower depths following urchin removal. Light readings under the *Desmarestia* canopy ranged from 5-80% of levels at the canopy surface, and were usually more than 10%. Evidently more light penetrated to the *Desmarestia* understorey than did the *Alaria* understorey. At 6-9m diversity was greater on the experimental transect than on the quicklimed transect. Both biomass and diversity (Figure 29) were generally low under control conditions,

The results of the survey, which was conducted to determine if the increase in macroalgal abundance occurred at other localities in Conception Bay, are presented in Table 7. A greater than 50% cover of fleshy macro-algae was present at 47% (7) of the sites. The species present at these sites were the same as those present in the control area (see page 25). At those sites with high fleshy algal cover the bottom invariably had abundant large (>50 cm. across) boulders, and/or abundant crevices. Fleshy macro-algae were largely absent from areas with only coralline encrusted, relatively smooth bedrock (i.e. lacking boulders or crevices).

2.6. The number of species and biomass of annual and ephemeral, versus perennial algae

There was little pattern in the relative abundance of annual and ephemeral *versus* perennial taxa under the different conditions when the species with mean biomass values less than .05 g quadrat^{-1} (the accuracy of the weighing balance) were included in the analysis (Figure 30). When these species were excluded a pattern emerged (Figure 31). Under the most uncertain conditions for recruitment and survival (0-2m with ice-scour; 2-3m and 6-9m with urchin grazing) the number of annual and ephemeral taxa exceeds the number of perennial taxa. The reverse appears to be true under the more favourable conditions for recruitment and survival (0-2m without ice-scour; 2-3m and 6-9m after urchin removal). Thus relative to the perennials, a larger fraction of annual and ephemeral taxa become rare under the more uncertain conditions of ice-scour and urchin grazing.

A greater biomass of annual taxa occurred under unstable conditions (0-2m, ice-scoured; both 2-3m and 6-9m under control conditions, and two mo after urchin removal), and greater biomass of perennial taxa occurred under more stable conditions (0-2m, no ice-scouring; and both 2-3m and 6-9m on the removal transects more than 9 mo. after urchin removal) (Figure 32).

2.7. Effect of ice-scouring on species composition at 0-2m

Table 8 presents biomass data for each species at 0-2m averaged by year. Ice-scouring during April of 1979 removed the dominant *Alaria*, and *Chordaria* became the most abundant species in scoured patches. *Chordaria* biomass was highest during the summer of 1979. *Chordaria* became senescent during the autumn of 1979, and the remaining individuals were removed by further ice-scouring during February of 1980. Recruitment by *Alaria* occurred mainly during late February and early March. *Saccorhiza* appeared during late March, and its biomass was highest during 1980. *Saccorhiza* became senescent by the following February (1981), when further *Alaria* recruitment occurred. During 1981 95% of the biomass was *Alaria*. In the absence of ice-scour during 1981 and 1982 *Alaria* remained dominant. Other species had higher biomass during years in which ice-scour occurred, but were evidently less sensitive to the timing of the scour episodes than were *Alaria*, *Chordaria* and *Saccorhiza*. This group of species includes *Chorda tomentosa*, *Ectocarpus* spp., *Petalonia fascia*, *Pilayella littoralis*, *Punctaria plantaginea*, *Scytosiphon lomentaria*, *Devaleraea ramentacea*, *Spongomorpha arcta*, and *S. aeruginosa*. *Laminaria digitata* was present, but patchy throughout the study. *Polysiphonia urceolata* was present throughout the study. Other species which were present in low abundance are presented in Table 8.

3. Urchin biomass, population structure, and the effectiveness of urchin removal

3.1. Urchin biomass on the control transect

Urchin biomass was greater at 2-3m than at 6-9m, and lower in samples from both the shallow (0-2m) macro-algal zone (Figure 33, Table 9), and the *Agarum/Ptilota* zone (Keats *et al.* 1982). Patches of urchins were also frequently observed along the fringe of the shallow algae zone (see Figure 2). These patches were sampled during the summer of 1979, and contained a geometric mean urchin biomass of 3280 g m^{-2} ($\log_{10}$ mean=3.515, s.e.=0.04, N=10). Such patches

(Figure 2) which were observed throughout the year, formed during calm periods and dispersed during rough seas. When sea conditions remained calm for long periods they created large bare patches within the shallow macro-algal zone, and/or decreased considerably the width of the zone within which fleshy macro-algae were abundant (see Himmelman 1969, 1980).

3.2. The percentage of the urchin biomass which was removed

Estimates of the overall effectiveness of urchin removal and exclusion (see **Materials and Methods**) are presented in Table 10. At 0-2m, where biomass was low, it was estimated that 92% of the urchin biomass was removed. Confidence limits were very large, however, ranging from a 52% increase to a 99.7% decrease in biomass. It is therefore unlikely that urchin removal had a significant effect on urchin biomass in the shallow macro-algal zone, where urchin biomass was low and the area difficult to access (due to wave surge). At 2-3m, where urchin biomass was greatest it was estimated that 93% of urchin biomass was removed. The 95% confidence limits ranged from 82 to 97%. At 6-9m, where biomass was intermediate between that of the 0-2m and the 2-3m samples, it was estimated that 88% of biomass was removed; confidence limits ranged from 66 to 96%. Table 10 also includes a coefficient of variation ($=s/\bar{X} \times 100\%$), the magnitude of which was greater under the treated condition than under the untreated condition for each depth range. This indicates that the urchin biomass was more patchy after removal than under control conditions at the same depth.

The percentage urchin biomass removed from the quicklimed transect was 94% (74% < 94% < 99%) at 2-3m (Table 11). At 6-9m the estimated percentage removal was 92%, but the 95% confidence limits were large (-60% < 92% <99.9%). The large confidence limits were probably the result of an increased patchiness due to the uneven application of the quicklime, and the small sample size (N=5). Urchin biomass data for the quicklimed transect are presented with the data from the other sites in Table 9, and Figure 33.

4. Urchin population structure

Urchin size frequency distributions from 0-2m, 2-3m, 6-9m, and 12-18m are presented in Figures 34, 35, 36, and 37 respectively. The smaller sizes (0-2 and 2.1-4 mm) were rare in the 0-2m and 12-18m samples. In general abundance of the smaller sizes was greater at 2-3m than at 0-2m , and peak abundance was at 6-9m.

No time related trends are obvious in the size frequency data from 0-2m (Figure 34). On the control transect at 2-3m there was a mode at 3 mm during the autumn of 1979 (Figure 35). During the spring of 1980 peak abundance was at 5 mm, and at 7 mm during the spring of 1981. During the summer of 1981 the mode was still at 7 mm, but absolute abundance had decreased. Abundance of the 11 mm size class at that time was greater than it had been previously. During the spring of 1982 the mode was at 5 mm, and abundance of the 7-15 mm size classes had decreased. During the summer of 1982 the mode was at 9 mm. On the experimental transect at 2-3m a mode at 3 mm disappeared after removal of larger urchins. This is probably a result of increased growth in response to the increase in macroalgal biomass, but any growth which took place was obscured due to the removal of urchins of more than *ca* 15 mm test diameter.

At 6-9m on the control transect the 1 mm size group was abundant during 1979-80, declined to very low levels by the spring of 1981, and remained low during 1982 (Figure 36). This decrease was followed by a decline in the abundance of the 3 mm size class, to near zero by the summer of 1982. The 5 mm size class had also decreased considerably by the summer of 1982. These data indicate that recruitment in 1979 and 1980 contributed to a high density of <2 mm urchins. An accumulation of those recruits in the 3 mm mode would account for an increasing trend evident in that mode until autumn 1980. Very low recruitment during subsequent years may have led to a decline in the abundance of the 1 mm size class, probably due to a combination of mortality and growth into the 3 mm size class. A decrease in the 3 mm size class showed a lag behind a decline in the 1 mm size class. There was very little change in the abundance of

the 5 mm size class until the summer of 1982, by which time it had decreased considerably. No modes progressing to the right were observed, indicating either very slow growth, high mortality, or both.

A similar trend was evident on the experimental transect (Figure 36). The peak remained at 3 mm during the summer of 1982, however, which may indicate reduced mortality of small urchins under the algal canopy. The data from the spring of 1982 indicated a tendency for increased growth of smaller urchins after removal of the larger individuals, but that was obscured at other times by the frequent removal of individuals larger than 15 mm test diameter.

The manual removal technique was inefficient with smaller ($<$ 15 mm) urchins. This contrasted with the quicklime technique which, while patchy in effect, yielded less size-selective mortality (Figs. 35, 36).

5. Biomass and density of other members of the herbivore guild

The total biomass of the herbivores other than urchins, in the study area was substantial (Table 9). It was generally greatest at 6-9m, where it ranged from 17-30 g m^{-2} (geometric means) in the control area, and from 30-54 g m^{-2} in the experimental area after urchin removal. In addition to *Strongylocentrotus droebachiensis*, the herbivore guild in the study area consisted of the polyplacophorans *Tonicella rubra*, *T. marmorea* and *Ischnochiton alba*, and the gastropods *Puncturella noachina*, *Acmaea testudinalis*, *Margarites helicinus*, *Lacuna vincta*, and *Skeneopsis planorbis*. Of these *Puncturella* and *Skeneopsis* were encountered only as solitary individuals in a small number of samples, and will not be considered further here. Some herbivorous amphipods may have been present in the study area, but were not quantified.

Tonicella rubra was the herbivore with the second greatest biomass in the study area (Table 12). Both biomass and density (Table 12) were negligible at 0-2m. At 2-3m on the control transect, biomass and density were greater than at 0-2m. *Tonicella rubra* was more abundant on the control than on the

experimental transect at this depth throughout the study. On the quicklimed transect both density and biomass were intermediate between biomass and density on the other two transects. Biomass and density were greater at 6-9m, where the species made up from 1% to 24% of the total herbivore biomass under control conditions. At this depth geometric mean biomass ranged from 8 to 32 g m^{-2}, and geometric mean density from 179 to 804 m^{-2}. There were no consistent between-transect or among sample period differences in either the abundance or the biomass of *T. rubra* at 6-9m. Biomass and density of *T. rubra* in the *Agarum/Ptilota* zone were similar to those at 6-9m.

Tonicella marmorea density in the study area was lower than that of *T. rubra* (Table 13). *Tonicella marmorea* was rarely present in samples taken shallower than the 6-9m depth range. Biomass and density reached maximum values from the mid barrens (6-9m) to the *Agarum/Ptilota* zone (12-18m). There was an increase in density and biomass on the control transect between the autumn of 1980 and the spring of 1981. The species was less abundant on the quicklimed transect than on the control or experimental transects. There were no other consistent among transect or sample period differences for this species. Neither *T. rubra* nor *T. marmorea* showed any detectable change in density or biomass in the removal areas following treatment (Tables 12, 13).

Ischnochiton alba was present in the study area only at 6-9m, but density and biomass were low, and it was very patchily distributed (Table 14). It is possible that *I. alba* was more abundant than the samples indicated, since it tends to be found mainly under large rocks, coming to the surface only at night.

Acmaea testudinalis was very patchily distributed, both spatially and temporally (Table 15). No consistent between transect differences were evident. The species comprised a small fraction of the total overall herbivore biomass under control conditions. The estimated *Acmaea* density was probably lower than its actual density, because large numbers of very small ($<$1-2 mm in length) *Acmaea* were often observed in quadrats, but were crushed because of their

delicate shells and the tenacity with which they cling to the substratum. It is evident, however, from Table 15 that *Acmaea* was most abundant at 6-9m, and rare in the *Agarum/Ptilota* zone.

Lacuna vincta abundance was greatest within the shallow portion of the study area during the autumn, particularly in the presence of macroalgae (Table 16). Although density was high at certain times, biomass was low under control conditions and was never more than 0.4 percent of the total herbivore biomass. On the experimental transect biomass, during the autumn-spring periods, was higher than on the control transect, and geometric means ranged up to 20 g m^{-2}. Peak settlement occurred during late August through September, with none during the winter to early summer period. Table 17 presents an estimate of percentage survival of *Lacuna* from the autumn of 1980 settlement on the control and experimental transects. Survival until spring was higher in the presence of macroalgae, and highest at 6-9m. Despite this trend only a small fraction of the recruited *Lacuna* survived into the summer of the year after they settled. Damage to some juvenile *Alaria* plants by *Lacuna* was observed in the study area (Figure 38), but no extensive grazing of algae by this gastropod was observed.

The pattern of distribution of *Margarites helicinus* within the study areas was similar to that of *Lacuna*, although abundance was lower (Table 18). Recruitment was observed at the same time of year, and abundance was highest in shallow water. Biomass of the species was low, and never amounted to more than 1.4 percent of the total herbivore biomass under control conditions. Table 19 presents an estimate of percentage survival of *Margarites* from the recruitment which occurred during the autumn of 1980. Although there were no significant differences in recruitment between transects, survival until spring was higher in the presence of macroalgae. Like *Lacuna*, only a small fraction of the recruited *Margarites* survived into the summer after they settled.

DISCUSSION

1. Summary of major trends

Interactions among urchin grazing, wave action, and ice-scour are important in structuring Newfoundland open Atlantic coast subtidal algal communities. In shallow water there is a zone of high macroalgal biomass, the lower limit of which varies with season and exposure to wave action (Himmelman 1985). Macro-algae are abundant in that zone because the dominant herbivore, *Strongylocentrotus droebachiensis*, is prevented from foraging effectively due to wave action. Within the shallow zone the patterns of biomass distribution among algal species vary considerably in relation to the presence or absence, and timing of ice-scour. In the absence of ice-scour, on relatively smooth bedrock where wave action is not extreme (eg. the study area), biomass in the shallow algal zone is dominated by the perennial kelp *Alaria esculenta*. Patchy disturbance by ice increased diversity by permitting colonization of the patches by otherwise rare or absent algae. Many species of algae show seasonal recruitment patterns, so the month of ice scour is an important determinant of species composition.

Within the urchin dominated zone a rich community of largely annual and ephemeral fleshy macro-algae develops in certain years, but in other years the zone is essentially bare of fleshy algae. The data available do not allow the determination of the causes of this year-to-year variation. Removal of urchins from this zone leads to a downward extension, into the upper part of the urchin dominated zone, of the *Alaria* community typical of the upper subtidal during years in which no ice-scour occurs. A reduction in the ability of urchins to forage, by an increase in wave action, may also lead to downward extension of the *Alaria* zone in some years (Himmelman 1985). A reduction in urchin grazing at

intermediate depths (6-9m) leads to the development of a flora dominated by the perennial, finely-branched alga *Desmarestia aculeata*. Both of these communities prevent the development of summer annuals.

The *Alaria* and *Desmarestia* communities occurred on both the manual removal and quicklimed transects, despite the difference in the time of urchin removal, suggesting that these associations might develop on a larger scale if a mass urchin mortality were to occur.

2. Effects of urchin removal on canopy species in Conception Bay

In eastern Newfoundland abundant *Alaria* is restricted to the shallow zone by urchin grazing. Domination of this shallow subtidal zone by *Alaria* in moderately to fully exposed areas is widespread in eastern Newfoundland (Himmelman 1980, Keats pers. obs.), at least in years between ice-scour episodes. *Alaria* is abundant in the immediate subtidal throughout much of its range in the north Atlantic Ocean. An *Alaria* zone is frequently found at sites with similar exposure in Nova Scotia (Mann 1972), Labrador (Wilce 1959, pers. obs. 1979-1984), Greenland (Lund 1959), Iceland (Munda 1975, 1977, 1979), the Faroes (Price and Farnham 1982), Norway (Jaasund 1965), and parts of the British Isles (Norton *et al.* 1977).

By the first spring after urchin removal *Alaria* formed most of the biomass in the upper portion of the removal areas. A number of features of the biology of *Alaria* may be important in allowing the species to develop and maintain dominance[7].

1. *Alaria* showed nearly synchronous recruitment. Although a few sporelings appeared throughout the winter-spring period, most

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[7]A dominant, as use here, refers to a species which exerts a strong influence on community structure. Thus the word applies to *Alaria* because it excludes most species from the community because of its closed canopy.

appeared during a two week period in February-March. *Alaria* recruitment is probably controlled partly by temperature, and in colder areas, such as Labrador, recruitment occurs over a more extended period (Himmelman *et al.* 1983a, R. Hooper,[8] pers. com.).

2. There was very high recruitment per unit area. A large number of sporelings appeared and completely carpeted the substratum. Such high recruitment ensures that there is very little space/light for competitors during the critical recruitment period.

3. *Alaria* can grow in a very dense stand with a closed-canopy, thereby limiting the amount of light reaching the substratum to $< 1\%$ of those at the canopy surface. This in turn probably limits the growth of potential competitors. A natural test of this hypothesis was provided by 1) ice-scour, and 2) the opening of the canopy by blade erosion. The abundance of other species increased in both of these instances.

4. *Alaria* grows rapidly. Within 4-5 wks of the appearance of *Alaria* germlings, many of the plants were more than 50 cm in length, and the canopy was essentially closed.

5. Most spores released by *Alaria* sporophytes probably settle and

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germinate into gametophytes within a short distance from the parent plant. Sundene (1961) transplanted mature *Alaria* to an area where it was not naturally present at Drøbak, Norway. Abundant juvenile sporophytes later appeared along a 10m stretch of shore, suggesting that the dispersal of large numbers of spores is limited to a scale of 10's of m. A single *Alaria* sporophyte was observed on the island of Surtsey in 1965, one year after the lava solidified. Once the "seed stock" was established, the population expanded rapidly, and by 1968 *Alaria* was the dominant species in a belt extending around the whole of the island (Jonson 1970). If most spores settle, and germinate into gametophytes which successfully reproduce near the parent population, this would reduce colonization into newly opened, large areas, but would result in recolonization and rapid reclosure of the canopy in openings near the parent population.

6. Its structural tissue (stiff but flexible stipe and midrib) allows *Alaria* to grow up off the substratum, above the level of lower stature species.

7. Although *Alaria* sporophytes are perennial, they need not survive for more than one year to reproduce successfully. The plants which arose in the first year after urchin removal produced sporophylls bearing reproductive sori during the following autumn-winter. Being perennial, however, sporophytes can persist for several years in the absence of disturbance, and monopolize the light resource (except in

late summer and autumn when the canopy becomes more open as a result of blade erosion).

Limited dispersal may also have been responsible for the initial lower limit of extensive *Alaria* following urchin removal in Conception Bay. On a local scale at steeply sloping sites, dispersal has two components: horizontal and vertical. The results of this study, and the study by Himmelman *et al.* (1983a) suggest that *Alaria* dispersal is better horizontaly than vertically. In the area studied by Himmelman *et al.* (1983a) the nearest *Alaria* was a large population 90m away on a wharf. *Alaria* colonized the shallow part, but not the deeper part of the removal plot. A limited horizontal dispersal on this scale (10's of m) could not account for this pattern, nor could a limited horizontal distance dispersal of spores account for the restriction of heavy *Alaria* recruitment to shallow water in Conception Bay. I observed that abundant *Alaria* colonized only the upper 1m of two ropes which marked the present study site. *Alaria* colonized the 6-9m depth range in the first year after urchin removal, but sporophytes were scattered, and the species made up only a small fraction of algal biomass. During the second year only a few sporelings were observed at 6-9m, primarily on the substratum near the base of the parent sporophytes which arose and produced mature sporophylls during the previous year. Some of these new recruits survived to maturity, resulting in a small increase in the size of the *Alaria* patch. By this time, however, the *Desmarestia aculeata* canopy was quite dense, and I speculate that it probably acted along with the limited depth dispersal to limit the further expansion of *Alaria* by limiting available light and/or space.

Desmarestia-dominated algal beds would probably develop in the mid-barrens in eastern Newfoundland, at least in the short-term (2-3y), if grazing pressure were reduced, for example by an urchin disease (Scheibling and Stevenson 1984) such as occurred in Nova Scotia. *Desmarestia aculeata* made up most of the algal biomass in the 6-9m depth range on both of the urchin-removal transects. *Desmarestia*-dominated beds also exist at several sites in Conception Bay, where my observations of very few urchins suggest that urchin grazing

pressure was reduced in comparison with grazing pressure on the control transect. Those *Desmarestia* beds have been stable for at least 8 years (pers. obs.).

The upper limit of abundant *Desmarestia* in the urchin removal areas was probably set by the closure of the *Alaria* canopy. The presence of *Desmarestia aculeata* at 2-3m during the first year after urchin removal, and on the control transect throughout the study shows that extensive *Desmarestia* was not restricted to the lower portion of the removal area by physical factors. Similarly, Santelices and Ojeda (1984) have shown that competition from *Lessonia vadosa* determined the upper limit of *Macrocystis pyrifera* at a site in southern Chile.

The presence of *Agarum* at 6-9m on the experimental transect and within the same depth range in the area studied by Himmelman *et al.* (1983), but in neither control area within this depth range, is somewhat suprising given its low dietary preference [possibly due to its high phenolic content (Steinberg 1980)] by urchins (Vadas 1977, Himmelman 1980, Larson *et al.* 1980, Keats *et al.* 1984). Why was *Agarum* not present in this depth range prior to urchin removal? Although this is speculation, the only explanation that fits what is known is that in barren areas, where urchin biomass is high, urchins graze the microscopic stages of *Agarum* along with the microscopic stages of other algae. In this case the *Agarum* would probably not be detected by the urchins, because of its small size and combination with other species. When the *Agarum* sporophytes reach a certain size, however, an urchin must graze entirely on *Agarum* with each feeding action if it is to include *Agarum* in its diet. Thus *Agarum* may have been excluded from the control area by indiscriminant grazing of its microscopic stages. Within the distinct *Agarum* zone urchin biomass is lower, but large urchins are still abundant (Keats *et al.* 1982). It is likely that frequent escapes of *Agarum* to a size refuge from grazing may account for the high abundance of *Agarum* within that zone. The higher densities of urchins at depths corresponding to the barren zone presumably graze all of the young stages, such that escapes to a size refuge are rare. In support of this adult *Agarum* are occasionally observed in the barren zone, and do not appear to incur much damage from urchin grazing. When

urchins were allowed access to the experimental transects they removed all fleshy macro-algae except for *Agarum* and *Ptilota*. Some of the *Agarum* plants survived for two years, despite very high densities of large urchins. Similar comments may apply to *Ptilota serrata*, which also is avoided by urchins (Himmelman 1980; Keats *et al.* 1984). *Ptilota* was present on the experimental, but not the control transect. Some *Ptilota* survived for at least one year after urchins had removed all other algae except for *Agarum*. It was very abundant in the zone (12-18m) where *Agarum* biomass was greatest.

3. Effects of urchin removal on species richness and diversity in Conception Bay

Following urchin removal at 2-3m there was an initial increase in the number of species. As the *Alaria* canopy became closed, however, the number of species (especially those which comprised more than one percent of biomass) declined, and diversity (H') decreased. Other large perennial algae (*Laminaria digitata* and *Desmarestia aculeata*), which were present during the first year, were replaced by *Alaria* by the second year after urchin removal. The *Alaria* canopy eliminated almost all light from the understorey, thus preventing the growth of competitors. This is likely the mechanism whereby species diversity was reduced during the later stages after urchin removal.

Seasonal changes in species richness and diversity were superimposed on this overall trend at 2-3m. This seasonal change in species richness was related to the erosion of the *Alaria* blades. During the late winter and early summer periods, the *Alaria* canopy reduced the light in the understorey to near zero. Species richness was low at that time. Following a reduction in the *Alaria* canopy by blade erosion during late summer, species richness increased in the urchin-removal areas. This blade erosion, exhibited by most Laminariales, may in this case be a response to high water temperature (Munda and Lüning 1977) combined with decreased nutrient levels (Buggeln 1974), which reduce growth and increase tissue destruction. Similarly, an increase in the abundance of understorey species associated with the seasonal degeneration of kelps (*Pterygophora californica*,

Laminaria setchellii, and *Dictyoneurum californicum*) has also been recorded in California (Dayton *et al.* 1984). Renewed growth of *Alaria* in the winter, correlated with decreasing water temperature and perhaps increasing nutrients (Buggeln 1974), again reduced the light reaching the understorey. This reduction in light in turn resulted in a decrease in species richness.

In contrast with the situation at 2-3m, and the general trend in urchin removal studies (see below), at 6-9m species richness and diversity increased and remained high after urchin removal. The *Desmarestia* canopy was never as completely closed as the *Alaria* canopy, and more light could penetrate to the understorey. The availability of light may have permitted several canopy forming (eg. *Alaria*, *Agarum* and *Laminaria*) and understorey species (eg. *Ceramium rubrum*, *Polysiphonia urceolata*, *Rhodomela confervoides*, and *Scagelia pylaisaei*) to co-exist with *Desmarestia*. In addition, a number of species (eg. *Ceramium*, *Polysiphonia flexicaulis* and *Ectocarpus*) grew as epiphytes on the profusely branched *Desmarestia*, and these contributed further to a higher species diversity at 6-9m than at 2-3m.

Intermediate levels of grazing would be expected to increase diversity (Paine and Vadas 1969; Lubchenco and Gaines 1981). The presence of the remaining urchins and the guild of molluscan herbivores, combined with a greater ease of foraging due to less wave surge, may have also contributed to the increased diversity at 6-9m after urchin removal.

4. Parallels with other studies of species richness and diversity after sea urchin removal

The pattern, observed during the present study, of an initial increase in species richness and diversity, followed by a decrease as one or a few species come to comprise most of the biomass is commonly observed when urchins are removed from barren areas. For example, Paine and Vadas (1969) removed urchins from intertidal and subtidal sites at Friday Harbor, Washington. There was an initial increase in diversity, but subsequently the intertidal sites became dominated by

Hedophyllum sessile, and the subtidal sites by *Laminaria complanata* and/or *Laminaria groenlandica*. Species richness in the intertidal remained high because of understorey species, but an extensive understorey did not develop in the subtidal. Paine and Vadas attributed this in part to the closure of a dense canopy in the subtidal. Breen and Mann (1976) eliminated urchins from a barren area within a kelp bed in St. Margarets Bay, Nova Scotia. Species richness was greatest during the first year after urchin removal, and then decreased as *Laminaria longicruris* came to dominate the removal plot. Foreman (1977) observed algal succession following the destruction of an algal community by *S. droebachiensis* in the Strait of Georgia, British Columbia. Species richness peaked 3-4 years after urchins were removed, and decreased to 26% of the maximum by year six. To simulate sea otter predation Duggins (1980) removed urchins from subtidal over-grazed areas in Alaska. Diversity of kelps increased in the first year, but declined to intermediate levels in the second year as dominance by *Laminaria groenlandica* increased. Pearse and Hines (1979) studied community development following natural mortality of urchins in central California. Within one year the area was dominated by a near monoculture of *Macrocystis pyrifera*.

Other studies indicate that species richness and diversity are reduced once a dense canopy is established because canopy-forming species can limit the amount of light reaching the understorey. For example, in the study by Pearse and Hines (1979 - cited above) the *Macrocystis* canopy was experimentally removed. This was followed by colonization by several species, thus demonstrating that its dense canopy reduced light levels in the understorey below those necessary for the growth and survival of other macro-algae. Harkin (1981), removed the distal portion of *Laminaria hyperborea* blades and obtained a significant increase in epiphyte biomass. Further evidence of the importance of light limitation by canopy-forming species was provided by Reed and Foster (1984), who demonstrated that light levels below a *Macrocystis pyrifera* canopy, or a surface *Macrocystis* canopy with a subsurface *Pterygophora californica* canopy are usually less than 1% of the light incident at the canopy surface. Removal of the

canopy resulted in a heavy recruitment by *Macrocystis*, *Pterygophora*, and *Desmarestia ligulata*, none of which recruited to the intact-canopy control sites.

5. Differences from the results of other urchin removal studies in the Northwest Atlantic

There have been differences among areas in the northwest Atlantic in the response of the algal community to urchin removal from barren areas. A major difference concerns the rôle of *Laminaria longicruris* in the communities which developed in response to reduced grazing pressure. In Nova Scotia *L. longicruris* colonized rapidly, and became the dominant species within a year (Breen and Mann 1976, Chapman 1981, Miller 1975, pers. obs. 1984). In the present study area the species did not appear in 2-1/2 years. The three *L. longicruris* sporophytes which appeared at the quicklimed site in Conception Bay may have resulted from spores derived from transplanted material, although it seems more likely that they arose from isolated spores transported from some distance. On the north shore of the lower St. Lawrence Estuary a few *L. longicruris* sporophytes appeared during the first 1-3 months after urchin removal (Himmelman *et al.* 1983a). Those plants attained a large size, but there was little or no further recruitment.

This difference is probably related to the availability of a spore source adjacent to the removal sites. In Nova Scotia *L. longicruris* was common in a shallow water refuge from urchin grazing (Chapman 1981, pers. obs. 1980)., so a spore source was available. The nearest *L. longicruris* population to the present study areas was at 1-3m depth on a wharf at Portugal Cove, 4.5 km away. The two species which became dominant at the experimental sites (*Desmarestia aculeata* and *Alaria esculenta*) were, however, present in the study area prior to the removal of urchins. A source of their spores was therefore present in the immediate area. *Laminaria longicruris* was absent on natural substrata in the area studied by Himmelman *et al.* (1983a). At that site it lacked a shallow water refuge from grazing because urchins graze right up into the intertidal. The species was, however, present on a wharf, 90m away from the removal plot. I

would speculate that were it not for the population of *L. longicruris* on the wharf, the species would not have occurred in the removal area. In any case, *L. longicruris* was absent from the subtidal fringe, and it was an unimportant component of the community which developed after urchin removal. Once the dense *Alaria* canopy was established, it presumably reduced further recruitment of *L. longicruris* into the area by eliminating light from the understorey (Himelman *et al.* 1983a).

The distance over which *Laminaria longicruris* is capable of dispersal may be small. If so this would explain the rapidity of *L. longicruris* colonization in Nova Scotia, its absence for 1-1/2 years in the Conception Bay urchin removal areas, and its poor initial recruitment at the removal site in the lower St. Lawrence estuary. The results of Chapman's (1981) study indirectly support the idea that *L. longicruris* has a limited potential for dispersal. He removed urchins during February of 1978 from four 10 m^2 quadrats located adjacent to, and 20, 30, and 40 m distant from an intertidal kelp fringe in St. Margarets Bay, Nova Scotia. *Alaria*, *L. digitata* and *L. longicruris* were common in the intertidal fringe, and colonized the removal areas. Colonization by these species began within two weeks in the plot adjacent to the fringe, but one, two, and three months respectively were required for colonization of the plots located 20, 30, and 40m distant. The depth range over which this experiment was conducted was not provided by Chapman (1981).

No data are available in direct support of the hypothesis of limited disperal for *L. longicruris*, but the Pacific species *Macrocystis pyrifera* has been studied from this point of view. *Macrocystis* water column spore concentrations are reduced considerably with distance from the parent plants, and spore concentrations, sufficient to establish enough gametophytes for a heavy recruitment of new soprophytes, occur at a maximum of 40m from a dense adult population (Anderson and North 1966). In California it was necessary to transplant either mature plants, germlings or gametophytes in order to establish *Macrocystis* in areas remote from existing *Macrocystis* beds (P.K. Dayton, pers.

com.[9]). Other species, once established, inhibited the recruitment of *Macrocystis* sporophytes (Dayton and Tegner 1984b, Dayton *et al.* 1984).

Laminaria longicruris was common in the shallow refuge from urchin grazing in Nova Scotia, so why is it absent from this refuge in eastern Newfoundland? It is present on a wharf at Portugal Cove and similar scattered locations throughout eastern Newfoundland. It occurs in Long Island Sound to the south, and into the Arctic (Taylor 1957), so we can therefore rule out temperature as a factor limiting its occurrence.

I propose a hypothesis to explain the absence of *L. longicruris* from the shallow refuge in eastern Newfoundland: The absence of *L. longicruris* is related to an interaction of the history of sea urchin grazing (long-term), with the limited dispersal ability of the species, its poor ability to compete with *Alaria* (and *Laminaria digitata*) in the shallow surf zone, and the periodic occurrence of severe ice-scour. The scenario which I propose is as follows: Long term grazing by urchins prevents *L. longicruris* populations from occurring below the shallow water refuge. It cannot colonize the shallow zone because of periodic heavy ice-scour, which eliminates all algae within that zone. Such heavy ice-scour did not occur during the present study, but it has been observed in the past. It results from a build up of hard, thick multi-year ice, which can scour to a depth of several meters (Hooper 1980). In the face of less severe ice-scour *L. longicruris* is probably unable to compete with *Alaria* (and possibly *L. digitata* at more exposed sites), even if spores did settle within the shallow fringe [*cf.* Himmelman *et al.* (1983a) for inability of *L. longicruris* to compete with an established *Alaria* canopy]. Thus *L. longicruris* is limited to a few widely scattered localities, and cannot disperse over long distances, even if conditions became favourable for colonization. In barren areas on the South coast of Newfoundland, where ice-scour rarely occurs, and in the Gulf of St. Lawrence (between Bonne Bay and the Bay of Islands), where scour is only by relatively thin, locally generated, first year

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ice, *L. longicruris* is common in the shallow water refuge from urchin grazing. For these reasons it seems likely that a *L. longicruris* dominated community would not develop in eastern Newfoundland, at least on a time scale of 3-4 years, if grazing pressure were reduced along extensive areas of coastline.

Extensive beds of *L. longicruris* exist in Newfoundland, for example at the head of Fortune Bay (Keats *et al.* 1982), and Bonne Bay (Hooper 1975). Extensive urchin dominated areas exist on the Gulf of St. Lawrence coast of Newfoundland, between Bonne Bay and the Bay of Islands (pers. obs. 1983-1984). On the open coast outside of Bonne Bay and the Bay of Islands *Laminaria longicruris* sporophytes are commonly encountered in the subtidal fringe, and as isolated patches on boulder and ridge tops, habitats from which the species is absent on the east coast. It seems likely that *Laminaria* dominated algal beds would develop in that part of the Gulf of St. Lawrence, and on the South Coast, in the event of a decrease in urchin grazing.

The response of the algal community to urchin removal in the lower St. Lawrence Estuary showed other differences from the response of the algal community in Conception Bay. Some of the differences are almost certainly related to the fact that the St. Lawrence Estuary experiences summer water temperatures considerably lower than those generally experienced at the Conception Bay site. Although *Laminaria digitata*, *L. longicruris*, and *Desmarestia* were present, neither extensive *Laminaria* nor *Desmarestia* developed in the area studied by Himmelman *et al.* (1983). Rather, below the zone of greatest *Alaria* biomass, there developed a mixture of *Agarum*, *Alaria*, *Ulvaria*, and *Ptilota*.

In the St. Lawrence estuary *Alaria* germlings appeared in July, soon after urchin removal, and attained a large stature by October (Himmelman *et al.* 1983). A second crop of germlings appeared in February. In Conception Bay *Alaria* germlings did not appear following urchin removal until December, were not abundant until February, and attained a large stature by April. *Alaria*

recruitment is greatest when water temperatures are low in Newfoundland (South and Hooper 1980), so the extended recruitment period of *Alaria* at the Quebec site was probably a result of the lower summer water temperature there.

Shortly after urchin removal *Ulvaria obscura* became abundant throughout the depth range studied by Himmelman *et al* (1983). It and other ulvoids were essentially absent from the present study area. In Newfoundland *Ulvaria obscura* is a winter/spring species (South and Hooper 1980), suggesting a dependence on colder water temperatures.

During the first 1-2 months after urchin removal at the present study site there was an enhanced growth or survival of certain summer annuals which were present at low abundance in the control area (eg. *Acrothrix novae-angliae*, *Eudesme virescens*, *Chordaria flagelliformis*), and an expansion of rhizoidal species (eg. *Scagelia corallina*, *Polysiphonia urceolata*) from cryptic habitats such as spaces among *Lithothamnion* uprights, as well as cracks and crevices in the corallines. Most of the summer annuals were gone by late September, and during the autumn, red algae dominated the substratum (Fig. 17). The extensive development of summer annuals, and the expansion of certain Rhodophyta did not occur at the Quebec site. The Quebec site experiences greater water turbidity, and less exposure to wave action than the Conception Bay site, differences which may also have contributed to differences in the effects of urchin removal. These differences serve to emphasize the importance of using caution in interpreting detailed local results in a regional or broader geographical context.

6. The importance of time scale

The results of a number of studies suggest that some trends observed in grazer removal studies are related to the temporal scale of observation (see Dayton and Tegner 1984a). For example, colonization and succession following release from overgrazing[10] has been studied over the longest time-frame by

[10]**Overgrazing** is used here to denote grazing levels which maintain algal biomass at very low levels.

Foreman (1977), who included a comparison with pre-grazing and ungrazed control areas. During an urchin outbreak in the Strait of Georgia, British Colombia, Canada, urchins (*Strongylocentrotus droebachiensis*) moved through the study area in a distinct "front" during 1973 (Foreman 1977). Following grazing the mean number of species per quadrat decreased by 50%, biomass by 65%, and diversity (H') by 60%. Annual and ephemeral algae made up most of the biomass during the initial stages of recovery. Many of the species which had been eliminated from the grazed site had reappeared by the second year, and biomass had returned to pre-grazing levels. Despite this recovery trend, 28 species collected during 1972 were not present in 1975, compared with 17 species in the control area. *Nereocystis luetkeana* an annual, large-stature kelp, which was uncommon in the pre-grazing or control area, was abundant at the recovering grazed site after 3 y. These facts indicate incomplete recovery after 3 y, and Foreman (1977) predicted that 4-6 y would be required to reach "ecological climax" (*sensu* Fishelson 1977).

It is important to note that most statements made thus far apply only to a relatively short time scale (3-4y). Given sufficient time it is likely that there would be further changes in community structure. For example, the potential does exist for the development of *Laminaria digitata* beds, or perhaps even *L. longicruris* beds, but if this were to occur it would likely be a long-term phenomenon. At exposed locations in eastern Newfoundland abundant *Laminaria digitata* is found mainly on vertical substrata, such as the sides of boulders, cliffs and surge channels. *Laminaria digitata* was common in each of these habitats in the vicinity of the study areas. Juvenile *L. digitata* were common in the *Desmarestia* understorey on both the experimental and quicklimed transects, and many patches of large plants occurred on the experimental transect. On the quicklimed transect, however, few large plants occurred. The failure of juveniles to develop beyond a small size was presumably a result of shading by *Desmarestia*, which was more dense on the quicklimed transect. This suggests the possibility that extensive mortality to *Desmarestia* could lead to *Laminaria* development, if the juvenile *Laminaria* were to grow

and mature. The *L. longicruris* sporophytes in the quicklimed area could possible give rise to an increasing population of that species, such that in the long-term a kelp bed community might develop.

7. Effect of ice scour on macro-algal species composition, diversity, and species richness in the shallow zone

The shallow zone with a high macro-algal biomass exists because urchin grazing is reduced by wave action (Himmelman 1985). Removal of urchins from that zone had no detectable influence on macro-algal biomass. Scouring by pack ice, was restricted to the intertidal and this upper subtidal algal dominated zone, where it had a measurable impact on the algal community. Ice-scour reduced algal biomass, but biomass returned to approximately pre-scour levels within a few months.

In the absence of ice-scour the shallow subtidal was dominated by *Alaria*, and both the biomass and the number of other species were low. Ice-scour cleared patches of *Alaria* from the substratum; other species appeared in the scoured patches, increasing the number and biomass of other species, and the evenness of biomass distribution among them. These data support predictions made by the intermediate disturbance model of community structure (Levin and Paine 1974).

Aspects of the disturbance regime which affect community response to disturbance include patch size, patch shape, the frequency of patch initiation, and the timing of disturbance events (Abugov 1982, Miller 1982, Paine and Levin 1981, Sousa 1979a,b, 1980, 1984). The results of the present study show that the timing of ice-scour determines its effect on the species composition of the algal community, although some of these differences may have been due to the combined effects of patch size, patch shape and the frequency of patch initiation in addition to the timing of disturbance. During 1979, when ice-scour occurred in April, *Chordaria* comprised 85% of the biomass in the more heavily ice-scoured area. During 1980, when ice-scour occurred in February, the scoured patches were colonized by *Alaria* sporelings, which resulted in a return to *Alaria*

dominance. *Chordaria* was less abundant during 1980 than 1979, but *Saccorhiza* was more abundant. Despite among year differences in species composition, species richness was not dependent on the month during which ice-scour occurred.

Factors which influence the stability of ecological communities have received the attention of ecologists in recent years (see Sutherland 1981, Connell and Sousa 1983, Dayton *et al.* 1984 for review). The *Alaria* dominated community has a low resistence[11] stability when perturbed by ice-scour; the species present, overall biomass and its distribution among species changed considerably as a result of ice-scour. The return to *Alaria* dominance after *ca* one year indicates a high degree of adjustment stability. Furthermore, the degree of adjustment stability (the resiliency) is influenced by the timing of ice disturbance, as indicated by a rapid return to *Alaria* domination when scour occurred in February, and a delay in the return of *Alaria* when scour occurred in April. Stability is thus not an innate property of the community; it depends not just on the magnitude and frequency of the perturbation, but also on the timing of its occurrence.

Based on the above observations, and on disturbance theory (White 1979, Paine and Levin 1981, Abugov 1982, Miller 1982, Sousa 1984), it is suggested that in the short-term ($<$4y) species richness of the upper subtidal would be greater if patchy but incomplete ice-scour occurred throughout the winter-spring period. That is, scouring in February would remove old *Alaria* sporophytes and lead to the formation of patches occupied by new *Alaria*, *Saccorhiza*, and species which are less seasonal. Scouring in April, if patchy and incomplete, would remove some of the old *Alaria* as well as the new *Alaria* and *Saccorhiza* plants, and patches would be colonized by *Chordaria* and other species. Patchy scouring during intermediate and later periods could presumably alter further the species composition, and diversity would be high.

On the south coast of Newfoundland, where ice-scour is rare [less than once

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[11]Terminology after Connell and Sousa (1983)

in 10-15 y (Markham 1981)], the high degree of domination by *Alaria* usually does not occur. There the shallow subtidal at sites receiving moderate to full exposure to wave action frequently has a rich community of perennial algae, which often includes *Alaria*, *Laminaria digitata*, *Laminaria longicruris*, *Chondrus crispus* and associated species (pers. obs., Hooper pers. com.). Although some of this difference may be due to the fact that the south coast is richer floristically than the east coast, it suggests that in the long-term absence of ice-scour or other major disturbance *Alaria* domination may decrease and a richer community may develop.

Based on the results of this study, and on the above observations from the south coast, a proposed relationship between community structure and ice-scour is presented in a simplified form in Fig. 39. The observations on the south coast suggest that in the absence of ice-scour or other large-scale disturbance the low diversity *Alaria* dominated community would develop into a high diversity community with many large perennial algae (pathway "A"). This increased diversity would be the result of an enrichment phase, as suggested by Fishelson (1977). This enrichment phase would consist of the colonization by epiphytes, and the formation and colonization of gaps in the *Alaria* stand which result from small scale disturbances involving the mortality of individual plants due to grazer damage, storm surge, or disease. Although I saw no evidence for this enrichment phase in the present study, the observations on the south coast of Newfoundland indicate that this is a likely scenario. Additionally, the potential would exist for the occurrence of species unable to survive in the periodically ice-scoured environment, and which on the open Atlantic coast lack a refuge below the ice-scour zone because of heavy urchin grazing. In eastern Newfoundland, pathway "A" is prevented by ice-scour and either "B" or "C," or a combination of "B" and "C" predominates depending on the timing of ice-scour. Although the short-term effect of ice-scour is to change a low-diversity *Alaria* dominated community to a rich community of annuals, the long-term extreme domination by *Alaria* may be dependant on periodic ice-scour. This periodic ice-scour prevents the development of a more diverse community (pathway "A"), and maintains the

system in a dynamic state (pathways "B" and "C"). The validity of these ideas should be subjected to further testing, particularly with studies conducted on the south coast of Newfoundland where ice-scour is rare, and in Labrador where it is an annual and prolonged event.

Chordaria was particularly prominent in patches scoured during April. On exposed shores of the Atlantic coast of Nova Scotia *Chordaria* is an important source of primary production in the intertidal zone (Rice and Chapman 1982). Probyn and Chapman (1982, 1983) have demonstrated that *Chordaria* possesses a very high V_{max} for nitrate and urea uptake, allowing it to take advantage of short-term pulses in the availability of dissolved nitrogen. In addition, *Chordaria* has a very low K_m for nitrate uptake (0.6 μg-at l^{-1}), indicating the ability to obtain nitrate at very low concentrations (Probyn and Chapman 1982, 1983). These adaptations make *Chordaria* particularly well suited to colonization and growth in areas scoured during the spring, just prior to a major decrease (Sandeman 1982) in nutrient concentration. Nutrient kinetics of the other species observed during the study have not been determined.

8. Comparison with other studies of ice-scour effects

Only one study provides data on species biomass-composition, richness and diversity in relation to ice scour. O'Clair (1981) compared species richness and species importance curves (the latter for molluscs only) for the intertidal of ice-scoured and unscoured islands in the Pribilof islands. Samples were taken during July-August following scour in April-May. Species richness for algae and molluscs was greater on the unscoured than on the ice-scoured islands. The unscoured islands also showed the greatest diversity of molluscs, as indicated by more species and a more even distribution of biomass among them. I suggest two reasons for the difference from the results of the present study. The sites were intertidal, and therefore subjected to more intense and more even scouring. The sites were also heavily scoured almost every year. Observations of the intertidal at the Newfoundland site indicate that scouring was more complete, and the diversity of species lower than in the less intensely and more patchily scoured upper subtidal.

This serves to emphasize the importance of the severity, and degree of patchiness of ice-scour in determining its effect on community structure.

A significant feature of the ice-scour which occurs on the open east coast of Newfoundland is that the ice is generated elsewhere (in the Labrador Sea and the Arctic) and drifts into the region under the influence of the Labrador Current and onshore winds. The formation of extensive local ice does not often occur in this region, so the coast usually lacks an ice-foot (ice frozen fast to the shore). If an ice-foot does occur in eastern Newfoundland it is usually short-lived, and does not build up, because of periodic above-freezing temperatures. An ice-foot usually occurs in more northerly regions, where ice is locally generated (Ellis and Wilce 1961). An ice-foot, when present, may serve to protect a portion of the intertidal and sometimes the upper subtidal from damage by the drifting ice. The intertidal and the upper subtidal were the most heavily impacted depths in the present study area.

The occurrence of alternating onshore, offshore, and along-shore winds and currents is an important factor which can increase the impact of ice-scour. Constant onshore winds pack the ice against the shore, and can limit scour in a manner similar to that of the ice-foot.

9. Algal abundance without urchin removal in Conception Bay

The increase in species richness at 2-3m on the control transect during the summer is probably due to a number of factors; one may be a seasonal cycle in urchin behavior. Bernstein *et al.* (1981) showed that urchins in St. Margarets Bay, Nova Scotia tended to be in hiding during the daytime in summer. Localized *Laminaria* regeneration was observed, but the new plants disappeared during the autumn when daytime foraging by urchins resumed. A second factor could be the formation, in the spring and early summer, of grazing "fronts" of sea urchins at the lower edge of the shallow zone. Reduced urchin biomass behind these "fronts" may have permitted macro-algal recruitment. A third factor may involve decreases in grazing potential due to an increased gonad size of urchins

(Himmelman 1985, Kuznetzov 1946, Keats *et al.* 1984). The size of urchin gonads is negatively correlated with depth in the study area (Keats *et al.* 1984). Reduced feeding as the test becomes full of gonad material may act along with wave action, and possibly more favourable light conditions, to permit a greater algal biomass and species richness at 2-3m than at 6-9m.

Most of the species which increased during the summer at 2-3m, and at 6-9m during 1982, were summer annual Phaeophyta. These include *Acrothrix*, *Chordaria*, *Dictyosiphon*, *Ectocarpus*, and *Giffordia*, which exist in cryptic phases during the winter. Most of these species also have vegetative short-cuts in their life history. The production (from these cryptic stages) of rapidly growing macroscopic phases, via spores or direct development, would thus account for the apparent increase in species richness during the summer.

Sea urchin grazing may actually increase the overall diversity of the community by preventing domination by *Alaria* along the upper edge of the urchin dominated zone, and thereby allowing the development of summer annuals such as *Acrothrix*, *Ectocarpus*, *Eudesme*, and *Tilopteris*, Summer annuals were fairly common along the upper edge of the urchin-dominated zone at the control site, even without the major increase in algal abundance, which occurred during 1982. Most of these summer annuals were excluded or reduced in abundance at 2-3m at the experimental sites by *Alaria*. At 6-9m the occurrence of these species in abundance was probably prevented by the predominance of other species, especially *Desmarestia aculeata*.

Increases in overall community diversity in the presence of heavy grazing has been reported in other areas. In New Zealand an increase in overall diversity was attributed to grazing by *Evechinus chloroticus* (Choat and Schiel 1982). In California grazing by the urchin *Centrostephanus coronatus* decreased small scale diversity in the patch in which it grazed, but increased diversity in the overall community by creating local areas suitable for otherwise rare taxa (Vance 1979).

The increase in species richness and algal biomass at 6-9m on the control

transect during 1982 was coincident with a decreasing trend in urchin biomass. It is not known if this trend represents a real decrease in urchin biomass, but if it does it could account for the increase in macroalgae. The fact that abundant urchins appeared in the autumn and eliminated all of the remaining algae, however, suggests that the apparent decrease in urchin biomass merely reflects an increased occupancy of cryptic habitat (eg. in crevices and under boulders), which was very patchily distributed and therefore not sampled quantitatively.

Since 1977 I have made extensive observations throughout Newfoundland and it is evident that a macro-algal increase, such as occurred within the middle of the barren zone during 1982 and 1983, often occurs in summer at many urchin dominated sites. The reasons for this increase remain to be determined, but may involve reduced grazing intensity, increased macro-algal growth rates, increased macro-algal colonization rates, acting singly or in combination. A much longer time-series of data, along with measurements of environmental factors and urchin behavior, will be necessary in order to explain fully this variability in macro-algal biomass within the urchin dominated zone.

10. Parallels between the effects of urchin grazing and ice-scour

Parallels exist between the effects of urchin grazing and the effects of ice-scour on the algal community. Three aspects of these parallels bear on the results of this study including (1) the longevity of the algae (annual and ephemeral *versus* perennial), (2) the available modes of reproduction (asexual short-cuts *versus* obligate sexuality), and (3) the ability of the algae to persist in cryptic phases, and asexually generate the macroscopic phase. The early stages following urchin removal, following ice-scour, and the temporary growth of macro-algae in the control area represent early succession.

The prediction that early successional species will be annuals or ephemerals, whereas later successional species tend to be perennials is supported by the results of the present study. The species which were the first colonizers after urchin removal were ephemerals (*Ectocarpus, Pilayella*, and annuals (*Acrothrix,*

Eudesme, Desmarestia viridis, Polysiphonia flexicaulis). Annual and ephemeral species were more abundant during years in which ice-scour occurred than thay were in its absence. Annual and ephemeral algae were most abundant in the control area during the macro algal increase which occurred during the summer of 1982.

These results are consistent with the results of a number of empirical studies which have also demonstrated this phenomenon. For example, short-lived annual algae were the first to appear in intertidal recolonization experiments conducted on Vancouver Island (Lee 1966). Annual and ephemeral species were the first to colonize when Dayton (1975) removed the dominant *Hedophyllum sessile* at a site in Washington, USA. Ephemerals colonized initially and perennial species were more abundant later in succession on an artificial substratum in a *Macrocystis pyrifera* forest in California (Foster 1975). Emerson and Zedler (1978) simulated natural disturbance in the California intertidal by brushing the substratum. Although there were strong seasonal effects on actual composition, annual species were generally the first colonizers. Ephemeral algae (*Enteromorpha, Polysiphonia, Ulva*) developed initially on mussel culture ropes in northwestern Spain, but subsequently the ropes became dominated by kelps (LaPointe *et al.*, 1981). Taylor and Littler (1982) removed a dominant sea anemone (*Anthopleura elegantissima*) in California, following which annual algae increased in abundance. Kain and Jones (1966) showed that the annual kelp *Saccorhiza polyschides* colonized urchin removal plots initially, but was later replaced by *Laminaria*. Duggins (1980) reported that the abundance and biomass of annuals were greatest in the first year after urchin removal, and declined as a *Laminaria groenlandica* canopy became closed. Removal of the canopy was followed by an increase in the abundance and biomass of annuals. Himmelman *et al.* (1983) noted that annual algae (*Chordaria flagelliformis, Desmarestia viridis, Petalonia fascia, Pilayella littoralis, Saccorhiza dermatodea, Spongomorpha arcta,* and *Ulvaria obscura*) were more abundant during the first year after urchin removal than they were during the second year.

Sousa (1979a,b,1980) studied the influence of disturbance, in the form of wave induced boulder movement, on macro-algal communities on large intertidal boulders in California. Annual species colonized newly overturned boulders, and there was an initial increase in diversity shortly after space was made available. Diversity decreased considerably after 2-3y if no further disturbance occurred, and a single species dominated between 60 and 90 percent of available secondary space. Reed and Foster (1984) showed that at a site in California with low levels of disturbance a few perennial species with a light-limiting canopy predominated. At another site, where disturbance was greater and more frequent, there was a diverse mixture of annual algae. O'Clair (1981) noted that ephemeral and annual algae were the most abundant in ice-scoured areas in the Pribilof Islands, Alaska, in contrast with non-scoured islands where large canopy-forming perennials were more abundant.

Annual and ephemeral algae have an advantage in early succession in that they tend to be fast growing, highly productive species, with relatively little non-photosynthetic structural tissue (Littler and Littler 1980, Steneck and Watling 1982). Perennial species, in contrast, often have a high degree of structural tissue, which results in lower productivity. Structural tissue reduces the probability of damage, and increases the alga's chance of surviving more than one season.

The prediction that early successional species will have vegetative short-cuts in the life history, whereas later successional species will generally lack such short-cuts is supported by the present study. All of the annual species (with the exception of *Desmarestia viridis* and *Saccorhiza dermatodea*) which were the initial colonizers after urchin removal, all of the species which were more abundant after ice-scour, and all those which predominated in the control area during the summer of 1982, have vegetative short-cuts [*Acrothrix* (Forward and South 1985), *Chordaria* (Kornmann 1962), *Dictyosiphon* (Bold and Wynne 1978), *Ectocarpus* (Mueller 1972), *Eudesme* (Bold and Wynne 1978), *Petalonia* spp. (Nakamura and Tatewaki 1975; Roelveld *et al.* 1974), *Punctaria* (Clayton and Ducker 1970), *Spongomorpha arcta*, (Tanner 1981), and *Scytosiphon* (Littler and

Littler 1983)]. Many of the perennials which colonized early also have vegetative short-cuts (*Ceramium, Polysiphonia urceolata, Rhodomela, Scagelia*) (Bold and Wynne 1978). In contrast, the perennial species which predominated after the first year (*Alaria, Agarum, Desmarestia aculeata, Laminaria digitata*) were obligately sexual (Bold and Wynne 1978). Vegetative short-cuts are advantageous for early colonization, because it is possible to produce large numbers of propagules without the necessity of going through the complete alternation of generations.

Vegetative short-cuts are likely to be particularly advantageous when the plants possessing them can produce macroscopic individuals, asexually from microscopic stages inhabiting cryptic microhabitat. Species with such cryptic phases capable of inhabiting surface irregularities in the substratum, and then producing uprights either directly or via dispersal of propagules, would also have an advantage over species which have to colonize from outside the disturbed area. Species with cryptic phases include *Chordaria*, *Dictyosiphon*, *Petalonia*, *Punctaria*, *Saccorhiza*, and *Scytosiphon*. *Spongomorpha aeruginosa* and *S. arcta* have a microscopic sporophyte which lives either endophytically or attached to the substratum (Kornmann 1972); it is also possible that they could survive as microscopic gametophytes. Little is known about the ecology of the microscopic stages of such algae, and field studies are urgently needed.

Devaleraea colonized after ice-scour, yet it evidently lacks the ability to disperse without sexual reproduction. It has a sexual cycle, involving a few-celled female, and a male which is isomorphic with the tetrasporophyte (van der Meer 1981). Tetrasporophytes develop on the female, and form a discoid holdfast on the substratum. Upright thalli develop from the discoid holdfast. A carposporophyte is lacking. The marked sexual dimorphism means that the males are much older than the females when they achieve fertility. In culture unfertilized females may develop directly into haploid tetrasporophytes, but the frequency and significance of this in nature is not known (van der Meer 1981). In the absence of ice scour, *Devaleraea* was uncommon in the study area. The

restrictions of the *Devaleraea* life history lead to the question "How was it able to colonize the scoured area?" According to J. van der Meer[12] (pers. com.) *Devaleraea* plants produce abundant carpospores and tetraspores. As well, both gametophytes and tetrasporophytes may persist in a basal crustose phase in cryptic habitats.

It is evident from the discussion presented here that a reduction in grazing, and the occurrence of ice-scour initiate succession. The trends observed during this succession, (the initial colonization by species characteristic of early succession, and the later reduction in their abundance as perennial canopy species become domminant), forms a common thread connecting grazing and ice-scour.

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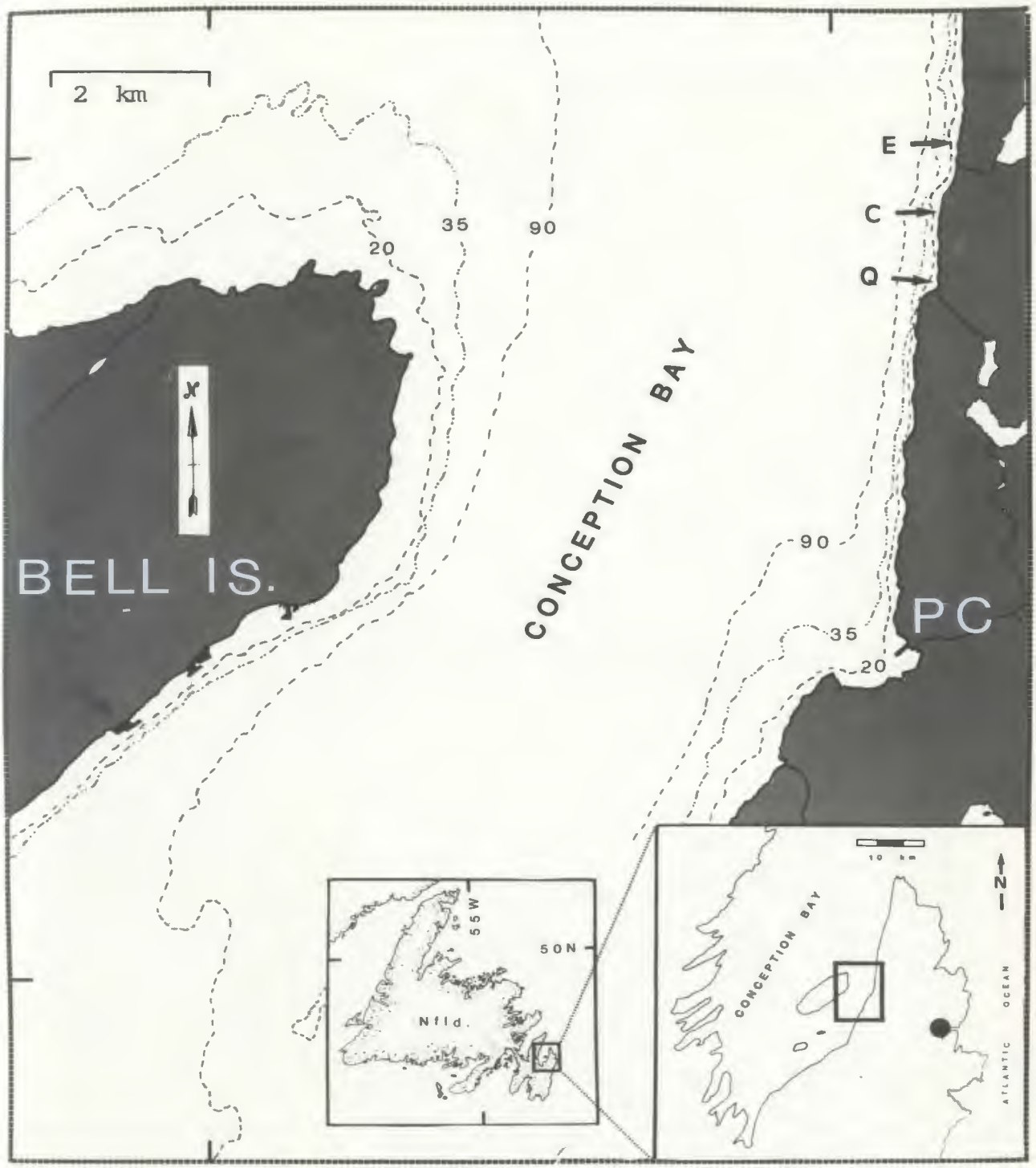
[12]NRCC, Atlantic Regional Laboratory, Halifax, Nova Scotia, Canada

Figures and tables

Fig. 1. Map showing the location of the study areas in Conception Bay {E=Experimental (manual removal) transect; C=Control transect; Q=Quicklimed transect; PC=Portugal Cove. Dot on inset map is location of St. John's. Depth contours in meters from nautical chart 4566}.


2 km
E
C
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35
90
20
CONCEPTION BAY
BELL IS.
PC
90
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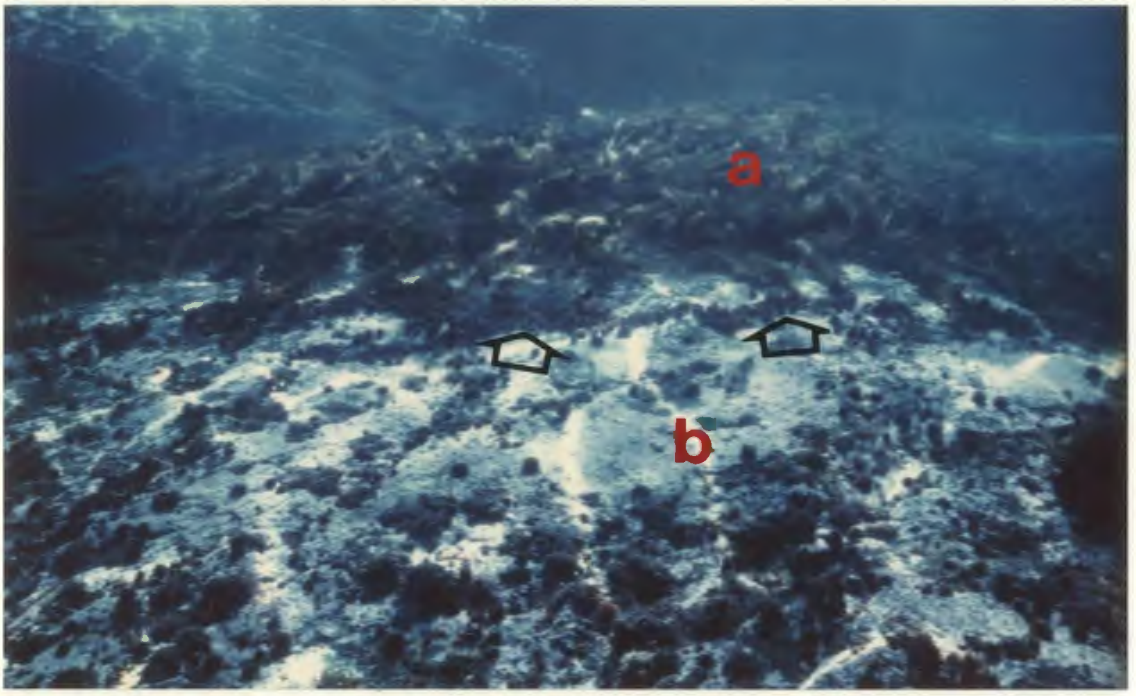
20
55W
50N
Nfld.
CONCEPTION BAY
N
ATLANTIC OCEAN

Fig. 2. Photographs illustrating the three main subtidal zones, typical of open Atlantic coast sites in Newfoundland. {a=The shallow fleshy macro-algae dominated zone, with a band of urchins along the lower edge (arrow); b=the urchin dominated "barren" zone; c=the deeper *Agarum/Ptilota* zone}.


a
b

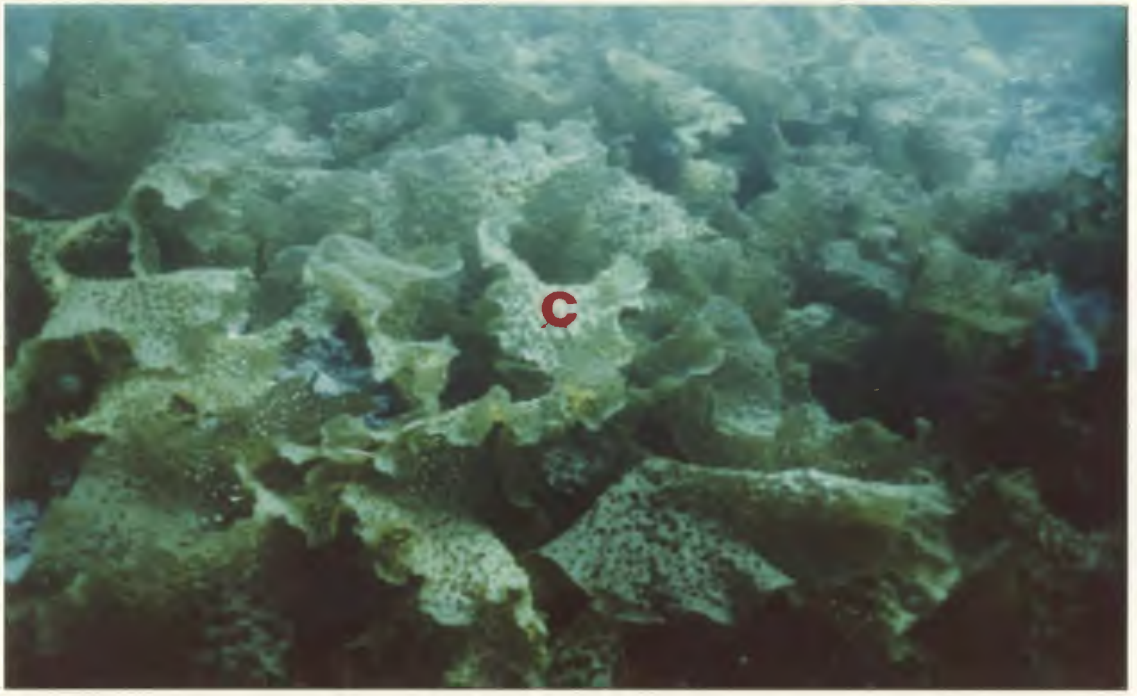

c

Fig. 3. Mean monthly frequency of wind in each of 5 categories ranging from calm (0) to fully onshore (4). Data are from Environment Canada, Atmospheric Environment service (1975). Categories: 0=calm; 1=offshore (E,SE,S); 2=onshore from within the bay, but sheltered by Bell Island (SW); 3=onshore from the across the bay (W), or slightly offshore but producing a light swell from outside the bay (NE); 4=fully onshore (N & NW). Mean monthly wind speed (averaged over all directions) is also included (the black line).

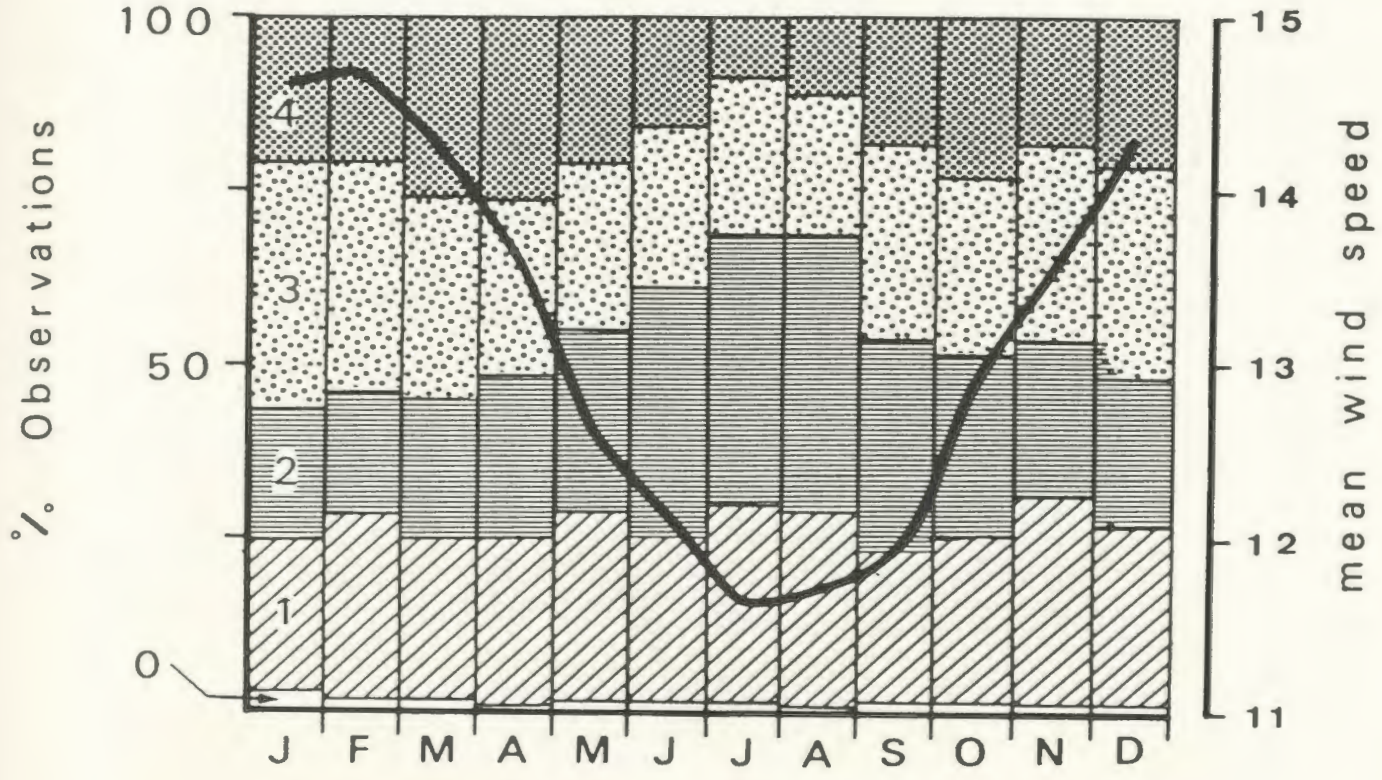

100
50
0
%. Observations
4
3
2
1
J F M A M J J A S O N D
15
14
13
12
11
mean wind speed

Fig. 4. Agricultural seed spreader attached to the back of the 12 m MV Elsie G. used for quicklime application.

Fig. 5. Diver sampling with the air dredge used in the present study.

Fig. 6. First year ice near the study sites (V) in Conception Bay during mid-April of 1979.


V

Fig. 7. Percentage cover of crustose coralline algae (including *Corallina* basal system) *versus* depth (averaged for both transects over sample periods: summer 1979, autumn 1979 and spring 1980). Key: PHYR=*Phymatolithon rugulosum*, LITG=*Lithothamnion glaciale*, CORAL=*Corallina officinalis* basal system, CLAT=*Clathromorphum circumscriptum*, PHYL=*Phymatolithon laevigatum*.

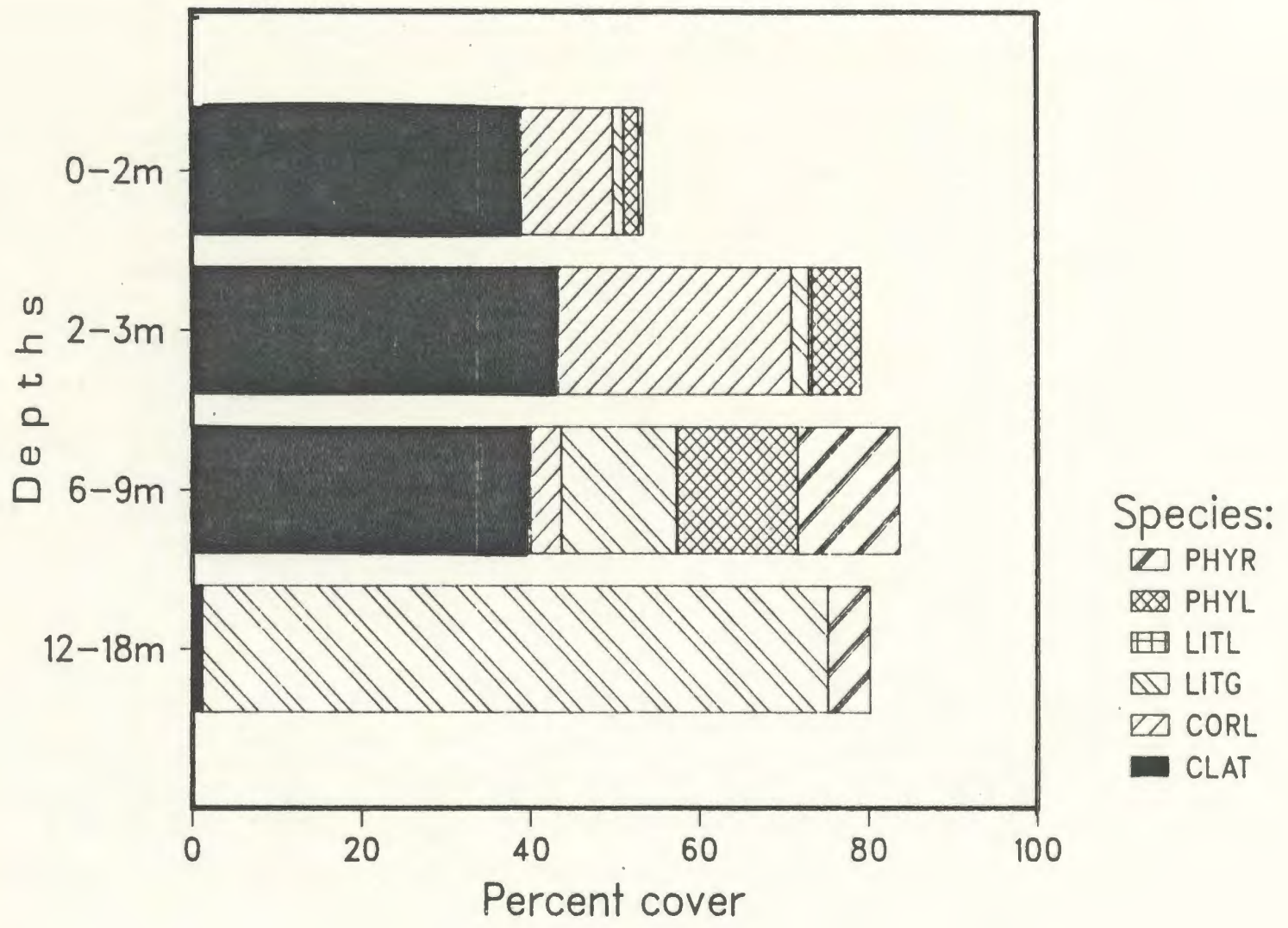

Depths
0–2m
2–3m
6–9m
12–18m
0
20
40
60
80
100
Percent cover
Species:
PHYR
PHYL
LITL
LITG
CORL
CLAT

Fig. 8. Total fleshy macro-algal biomass for each transect, depth, and sample date [geometric mean (g m^{-2}) $\pm$ std. err.]. Vertical line indicates the time of urchin removal from the experimental transect.

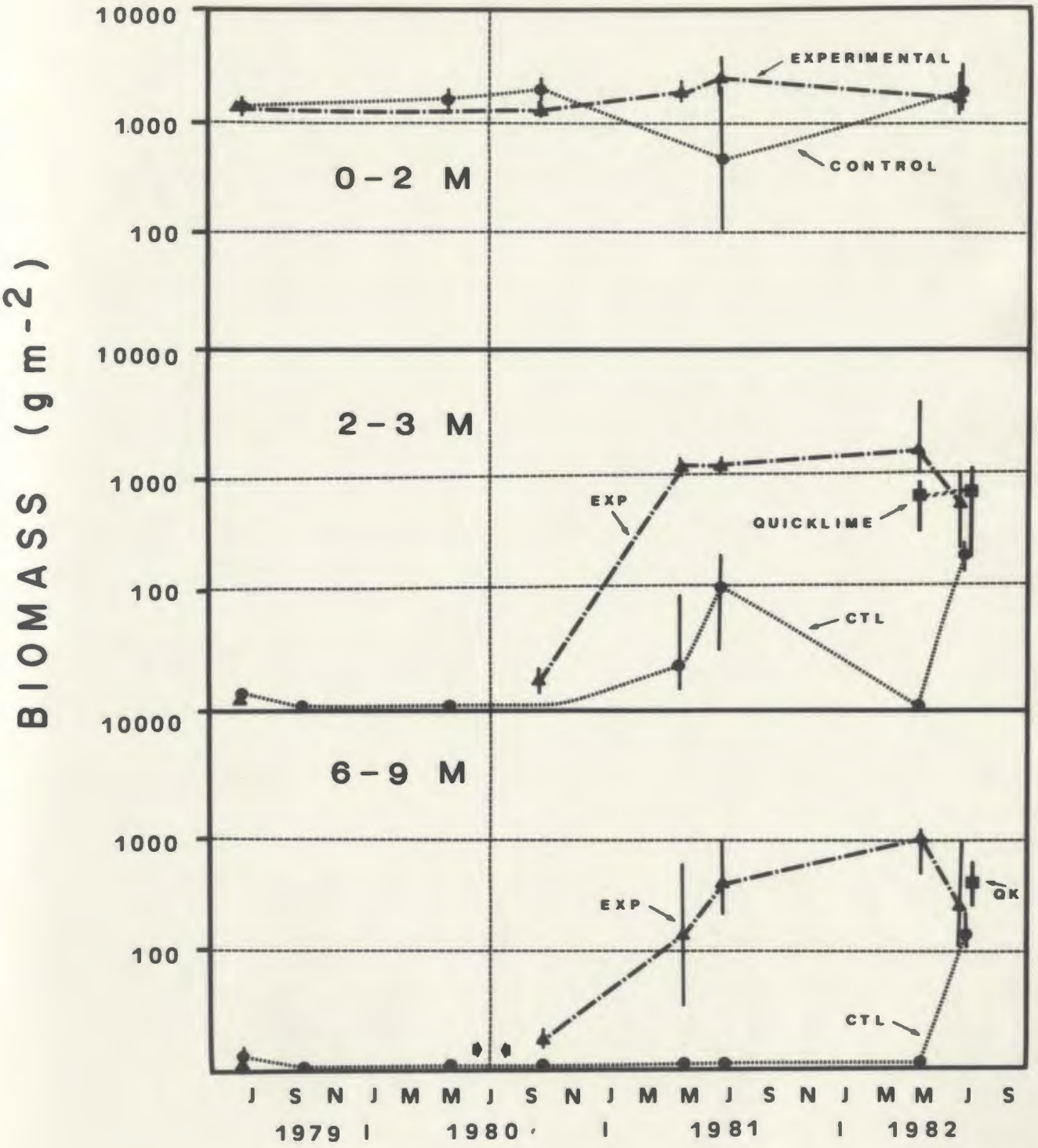

BIOMASS (g m-2)
10000
1000
100
0-2 M
EXPERIMENTAL
CONTROL
10000
1000
100
2-3 M
EXP
QUICKLIME
CTL
10000
1000
100
6-9 M
EXP
QK
CTL
J S N J M M J S N J M M J S N J M M J S
1979 1980 1981 1982

Fig. 9. Cluster analysis of macroalgal biomass data. Sample sets were clustered on the basis of $\log_{10}$ mean for each species. Key: [FORMAT: Transect, Depth, Sample period (1=E,0-2m,Sum79; 2=C,0-2m,Sum79; 3=E,0-2m,Aut80; 4=C,0-2m, Spr80; 5=C,0-2m,Aut80; 6=E,0-2m,Spr81; 7=E,2-3m,Sum81; 8=E,2-3m,Spr81; 9=E,0-2m,Sum81; 10=E,0-2m,Sum82; 11=C,0-2m,Sum81; 12=E,2-3m,Sum82; 13=E,2-3m,Spr82; 14=C,0-2m,Sum82; 15=Q,2-3m,Sum82; 15=Q,2-3m,Spr82; 17=E,2-3m,Sum79; 18=E,6-9m,Sum79; 19=C,2-3m,Sum79; 20=C,6-9m,Aut80; 21=C,2-3m,Spr82; 22=C,6-9m,Spr80; 23=C,6-9m,Spr82; 24=C,2-3m,Spr80; 25=C,6-9m,Spr81; 26=C,6-9m,Aut79; 27=C,6-9m,Sum81; 28=C,6-9m,Sum79; 29=C, 2-3m,Sum79; 30=E,2-3m,Aut80; 31=E,6-9m,Aut80; 32=C,2-3m;Spr81; 33=Q, 6-9m,Sum82; 34=C,2-3m,Sum81; 35=C,2-3m,Sum82; 36=E,6-9m,Sum82; 37=E, 6-9m,Spr81; 38=E,6-9m,Spr82; 39=E,6-9m,Sum82; 40=E,6-9m,Sum81; 41=C,12-18m, Spr79; 42=C,12-18m,Spr80; 43=C,12-18m,Spr81). Note: 12-18m data are from samples used for Keats et al. 1982].

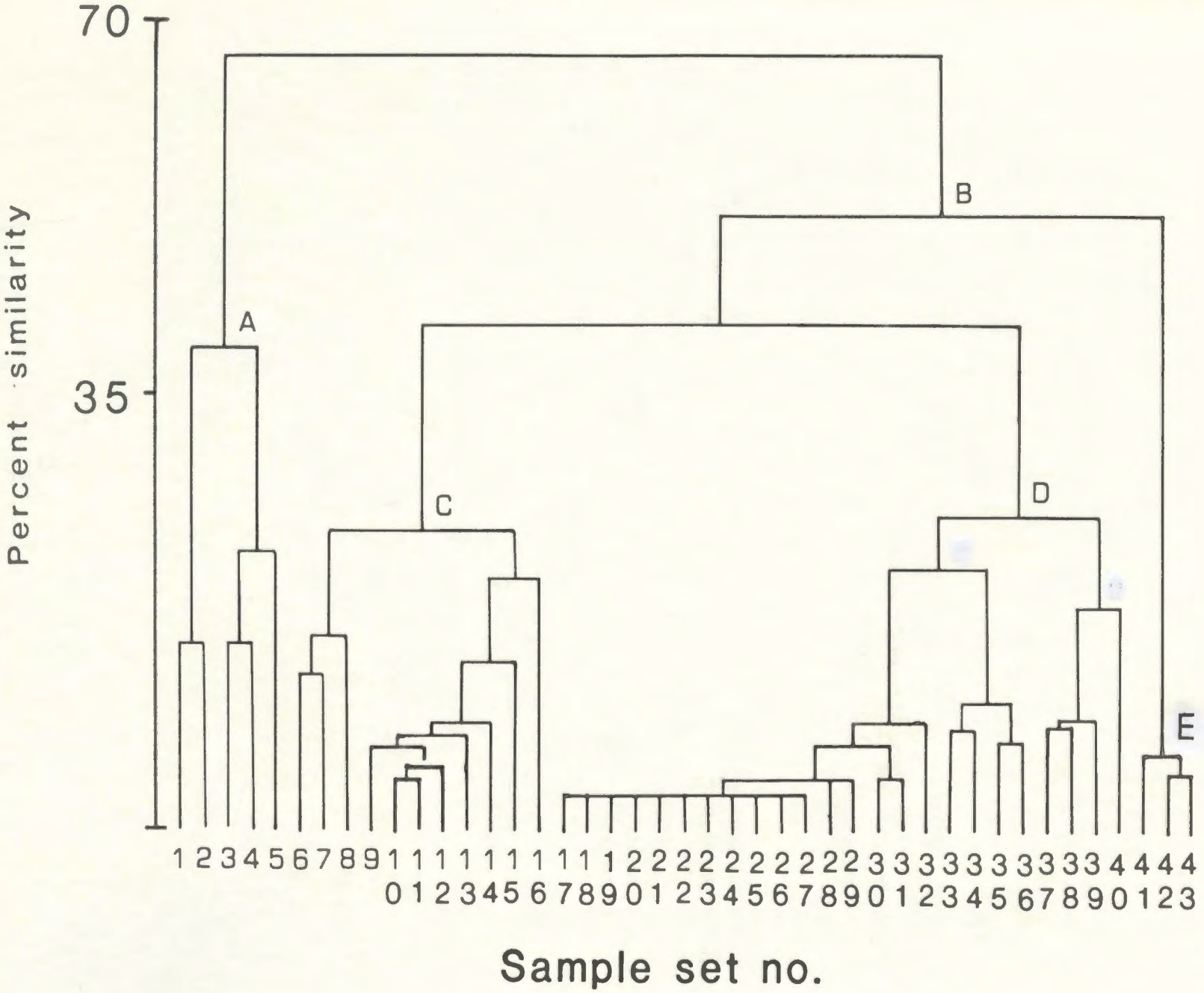

70
35
Percent similarity
A
B
C
D
E
1 2 3 4 5 6 7 8 9 1 1 1 1 1 1 1 1 1 2 2 2 2 2 2 2 2 2 3 3 3 3 3 3 3 3 3 4 4 4 4
0 1 2 3 4 5 6 7 8 9 0 1 2 3 4 5 6 7 8 9 0 1 2 3 4 5 6 7 8 9 0 1 2 3
Sample set no.

Fig. 10. Biomass of *Alaria esculenta versus* sample month [geometric mean (g m^{-2}) $\pm$ std. err.] ($\square$ =Control transect, $\triangle$ =Experimental transect, $\times$ =Quicklimed transect). ($\pm$ std. err.).

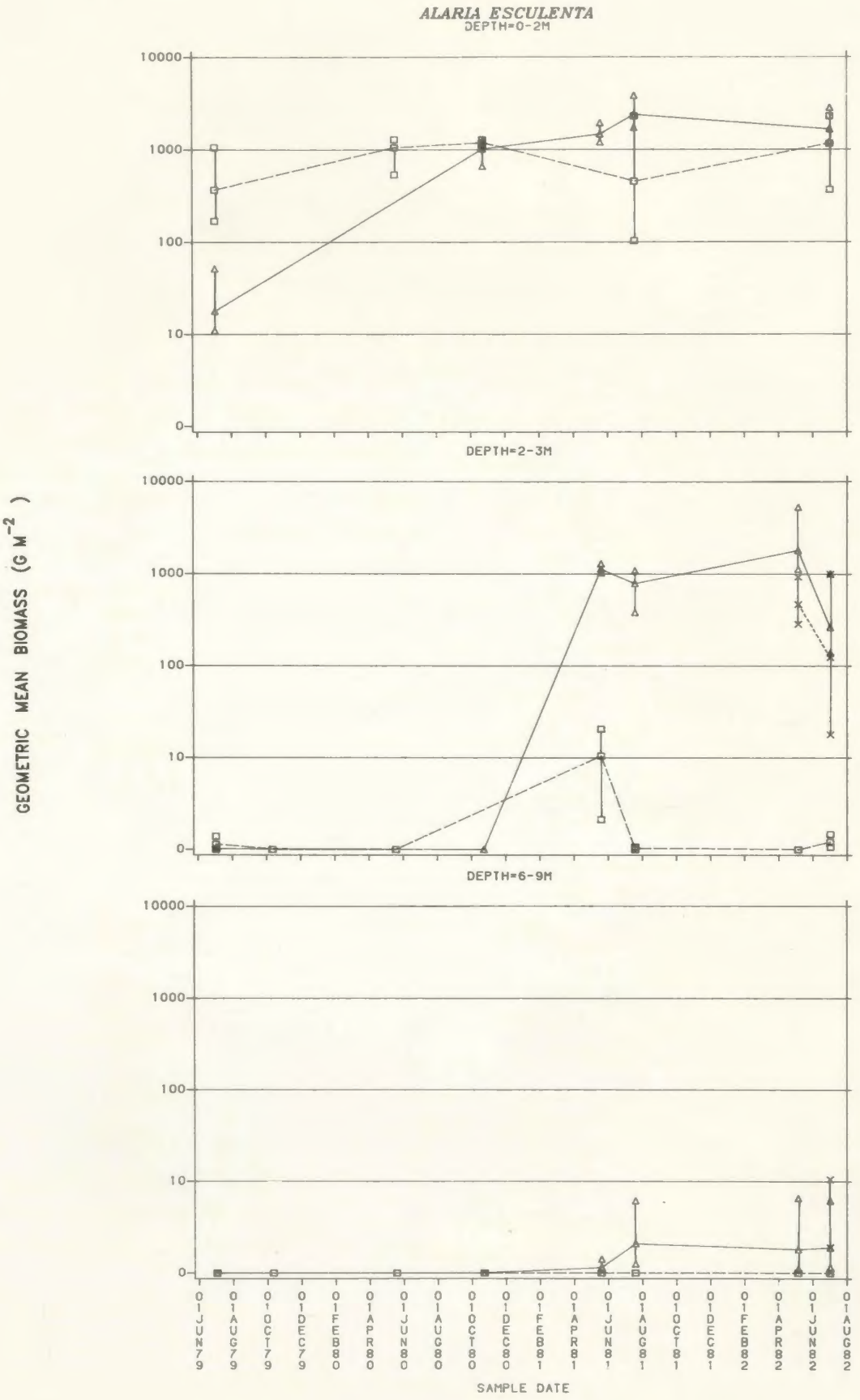

ALARIA ESCULENTA
DEPTH=0-2M
DEPTH=2-3M
DEPTH=6-9M
GEOMETRIC MEAN BIOMASS (G M^{-2})
10000
1000
100
10
0
01JUN79
01AUG79
01OCT79
01DEC79
01FEB80
01APR80
01JUN80
01AUG80
01OCT80
01DEC80
01FEB81
01APR81
01JUN81
01AUG81
01OCT81
01DEC81
01FEB82
01APR82
01JUN82
01AUG82
SAMPLE DATE

Fig. 11. Biomass of *Desmarestia* spp. *versus* sample month [geometric mean (g m^{-2}) $\pm$ std. err.] ($\square$ =Control transect, $\triangle$ =Experimental transect, $\times$ =Quicklimed transect). ($\pm$ std. err.).

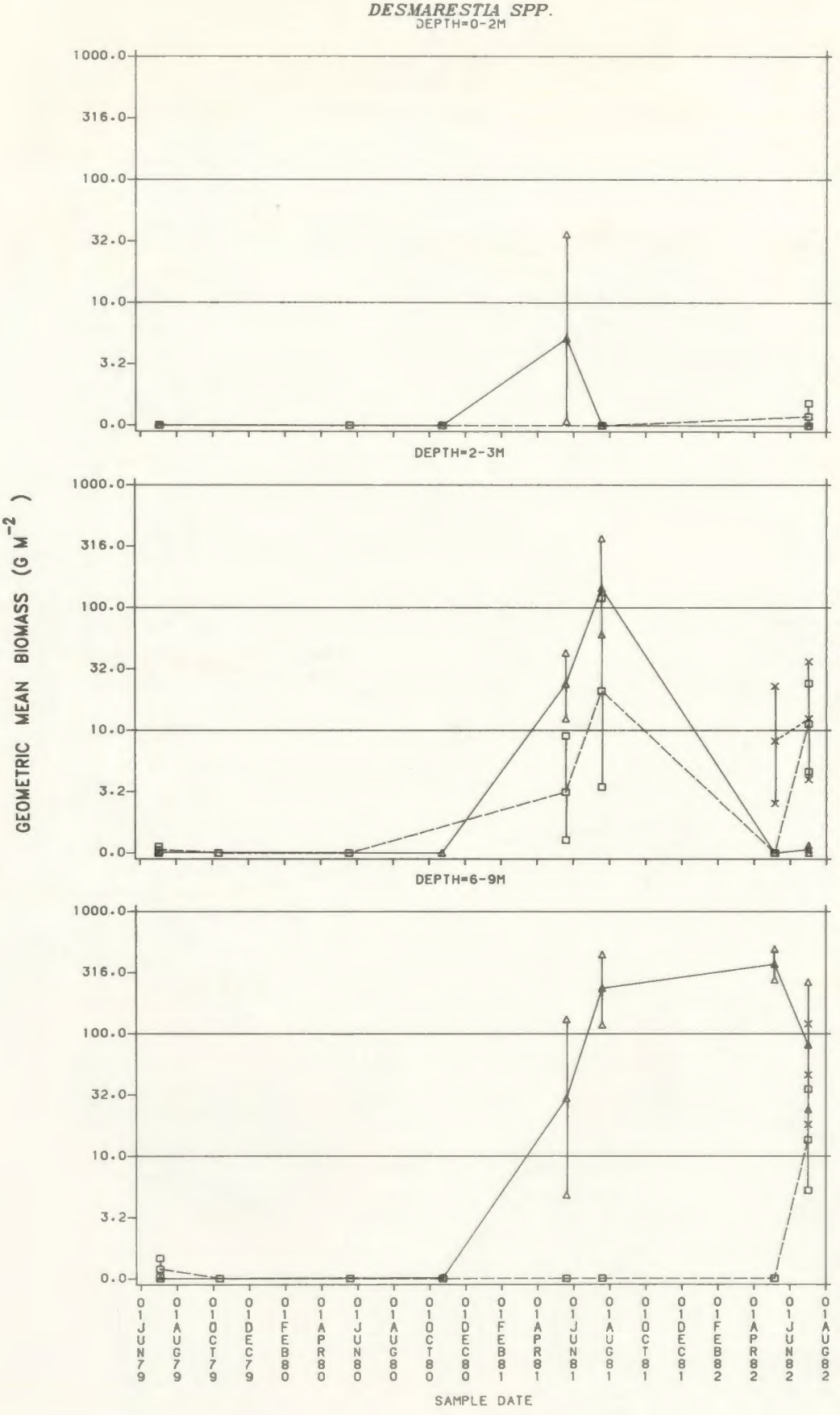

DESMARESTIA SPP.
DEPTH=0-2M
DEPTH=2-3M
DEPTH=6-9M
GEOMETRIC MEAN BIOMASS (G M^{-2})
1000.0
316.0
100.0
32.0
10.0
3.2
0.0
01JUN79
01AUG79
01OCT79
01DEC79
01FEB80
01APR80
01JUN80
01AUG80
01OCT80
01DEC80
01FEB81
01APR81
01JUN81
01AUG81
01OCT81
01DEC81
01FEB82
01APR82
01JUN82
01AUG82
SAMPLE DATE

Fig. 12. Biomass of *Laminaria digitata versus* sample month [geometric mean (g m^{-2}) $\pm$ std. err.] ($\square$ =Control transect, $\triangle$=Experimental transect, $\times$ =Quicklimed transect). ($\pm$ std. err.).

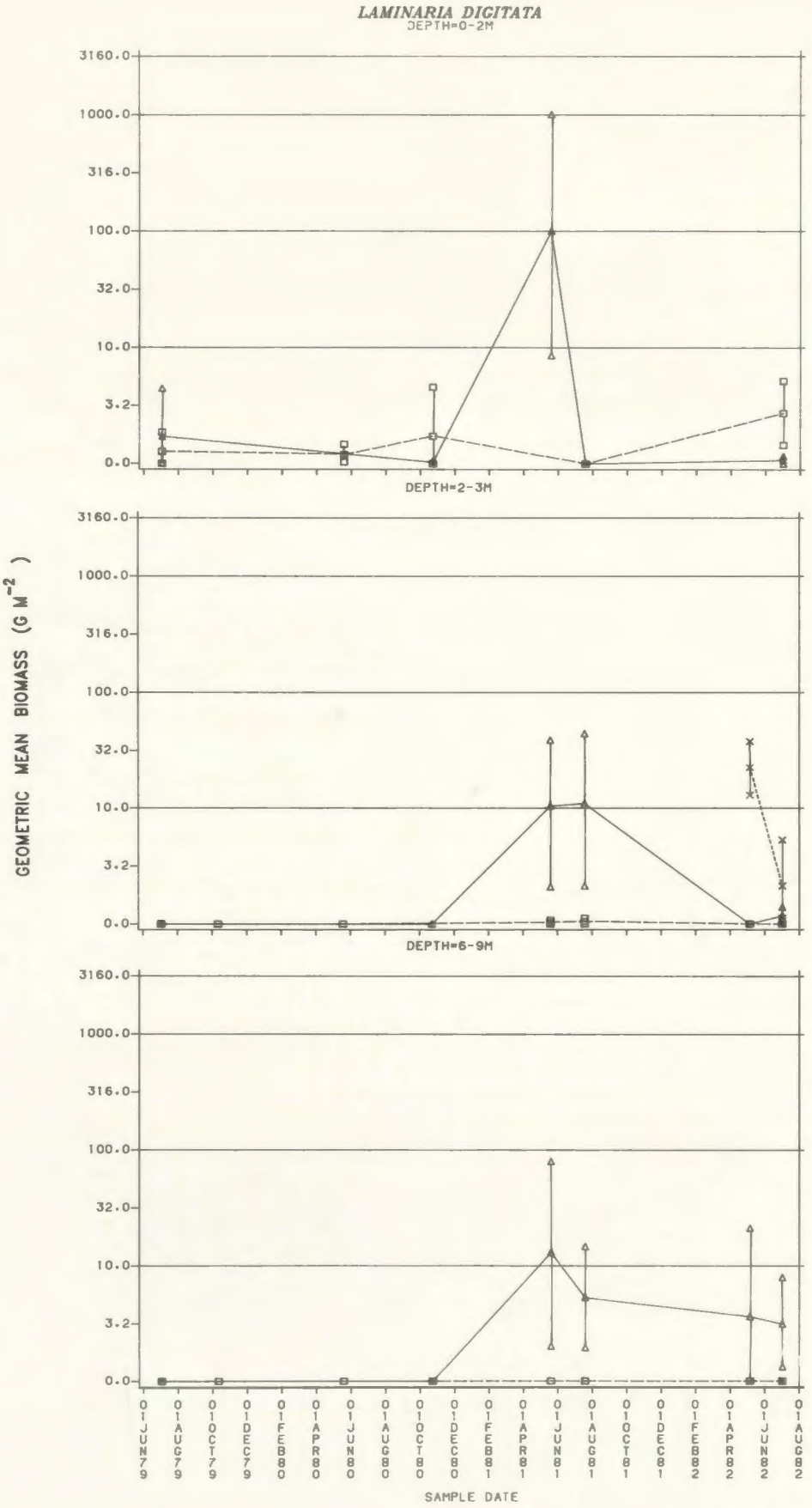

LAMINARIA DIGITATA
DEPTH=0-2M
DEPTH=2-3M
DEPTH=6-9M
GEOMETRIC MEAN BIOMASS (G M-2)
3160.0
1000.0
316.0
100.0
32.0
10.0
3.2
0.0
01JUN79
01AUG79
01OCT79
01DEC79
01FEB80
01APR80
01JUN80
01AUG80
01OCT80
01DEC80
01FEB81
01APR81
01JUN81
01AUG81
01OCT81
01DEC81
01FEB82
01APR82
01JUN82
01AUG82
SAMPLE DATE

Fig. 13. Photograph illustrating patches of *Desmarestia* spp. (D) on the control transect (summer 1979). Arrow indicates a winter flounder (*Pseudopleuronectes americanus*). Note also the abundant *Corallina officinalis* (C).

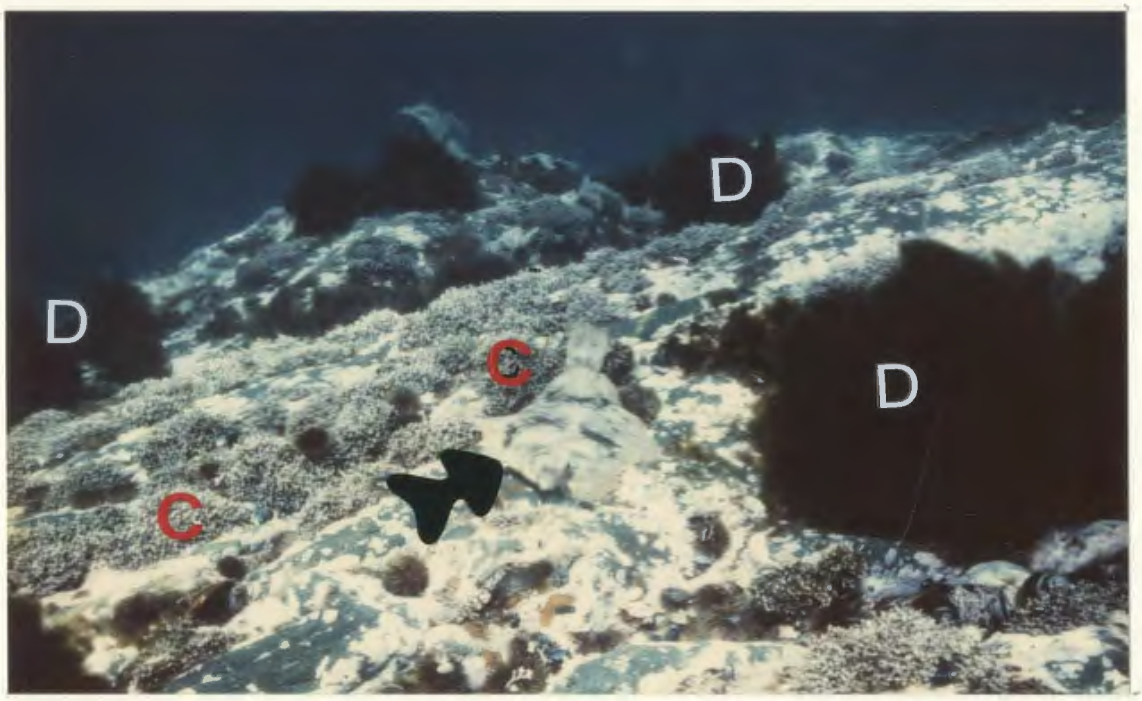

D
D
C
D
C

Fig. 14. Photograph illustrating growth of *Urospora wormskjoldii* (arrow) on the tops of ridges on the control transect during the spring of 1981.

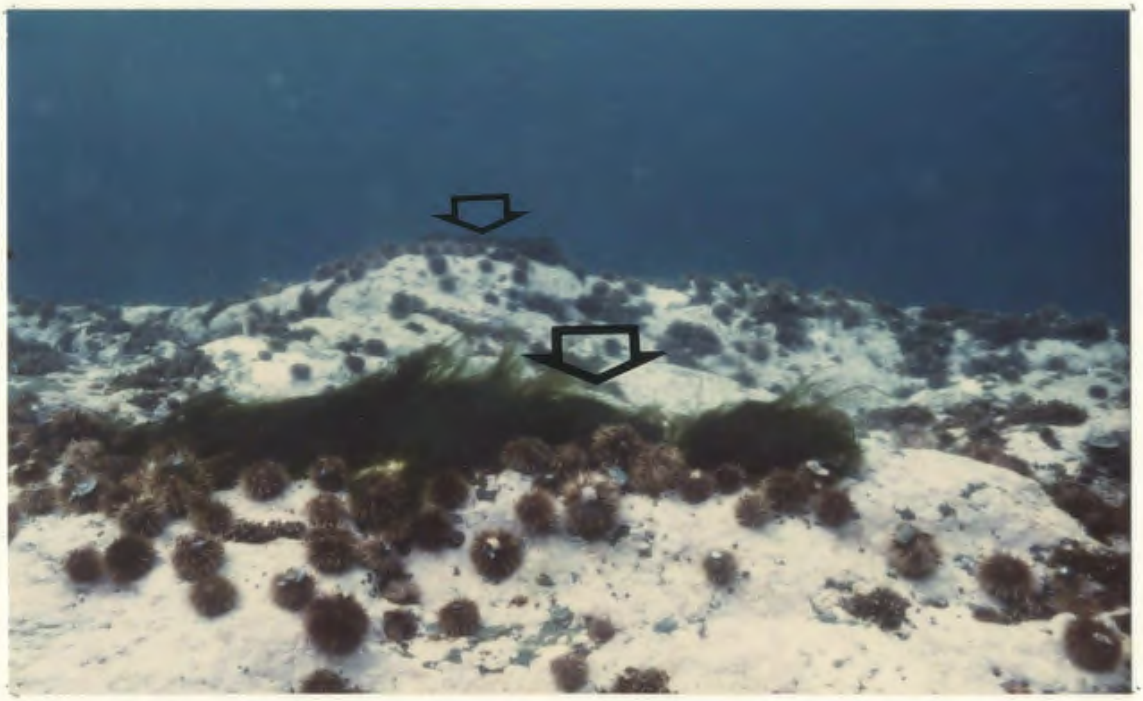


Fig. 15. Photograph illustrating heavy growth of *Ectocarpus siliculosus* (tail-less arrow) and associated species, especially *Eudesme virescens* (arrow with tail) at 2-3m on the control transect during the summer of 1982.

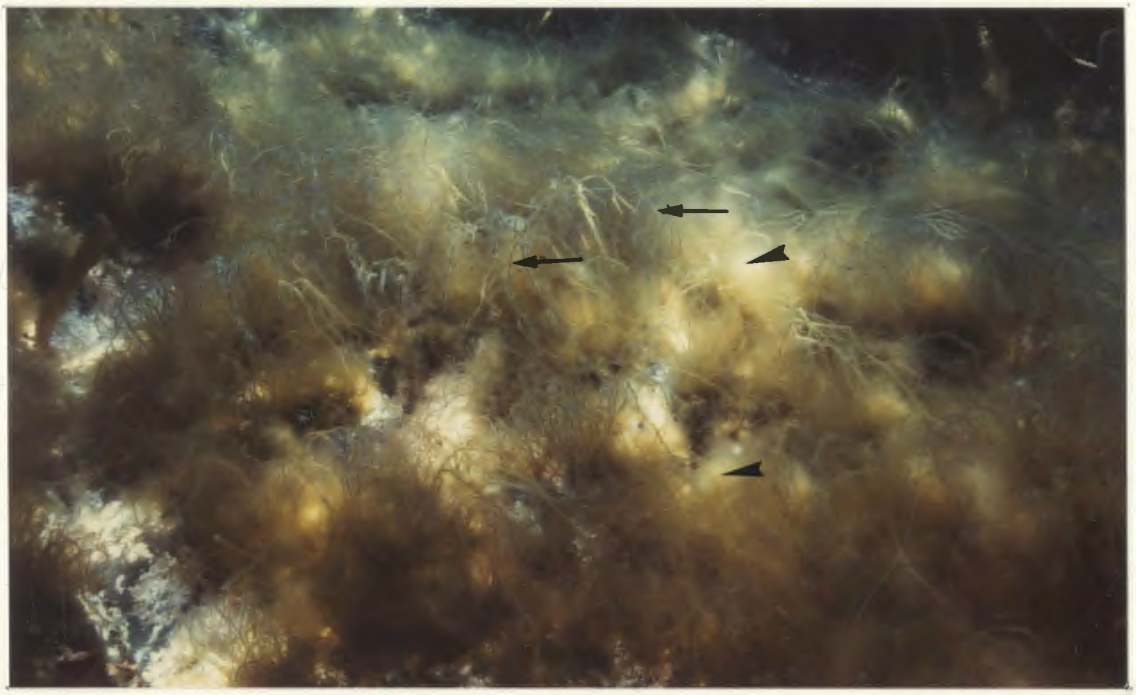


Fig. 16. Photograph illustrating the diatom and *Ectocarpus/Pilayella* turf present during the earliest stage after urchin removal. The abundant fish are cunners (*Tautogolabrus adspersus*).

Fig. 17. Photograph illustrating the occurrence of certain Rhodophyta (arrows) during the first autumn following urchin removal on the experimental transect.

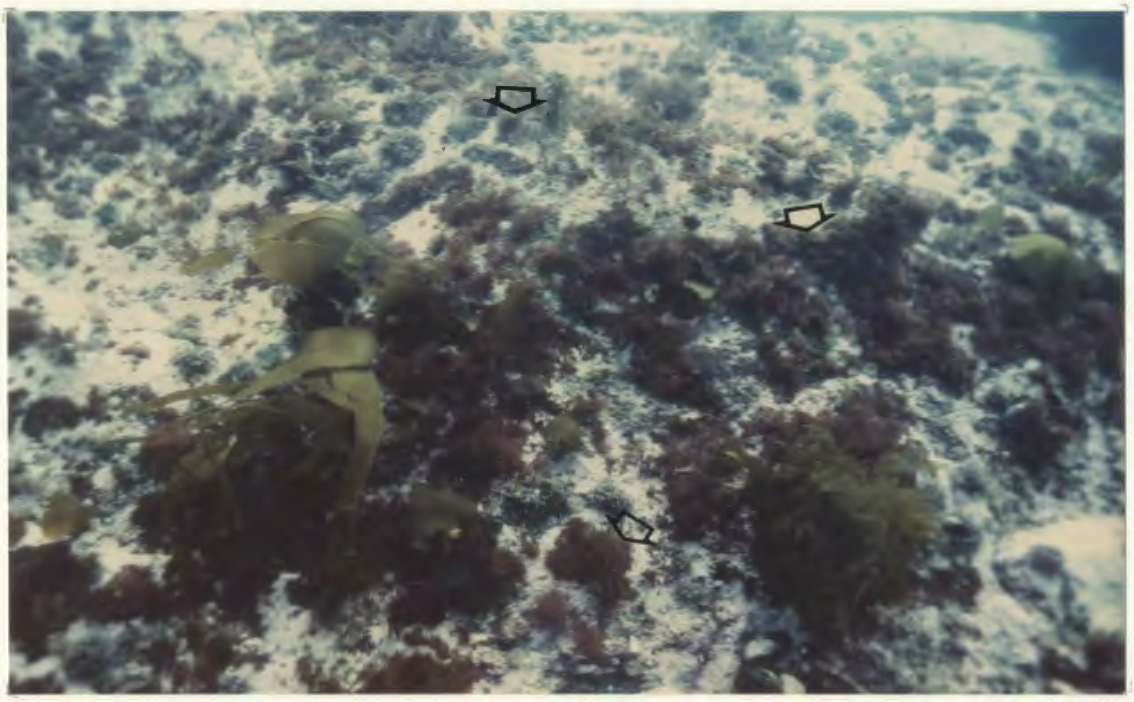


Fig. 18. Photograph illustrating (a) colonization by *Alaria esculenta* (tail-less arrows) during March of 1981, and (b) the same area one month later. The fish in (b) is a male lumpfish (*Cyclopterus lumpus*).


b

Fig. 19. Photograph illustrating *Agarum* (a) in the 6-9m depth range in the removal area during March of 1981. Note also *Alaria esculenta* (e), *Laminaria digitata* (l), and *Desmarestia aculeata* (d). The fish are cunners (*Tautogolabrus adspersus*).


d
l
e
a

Fig. 20. Photograph illustrating abundant *Desmarestia aculeata* (d) in the 6-9m depth range, and some of the large algae existing with it during the spring of 1981 (a=*Alaria esculenta*, b=*Laminaria digitata*, c=*Agarum cribrosum*).

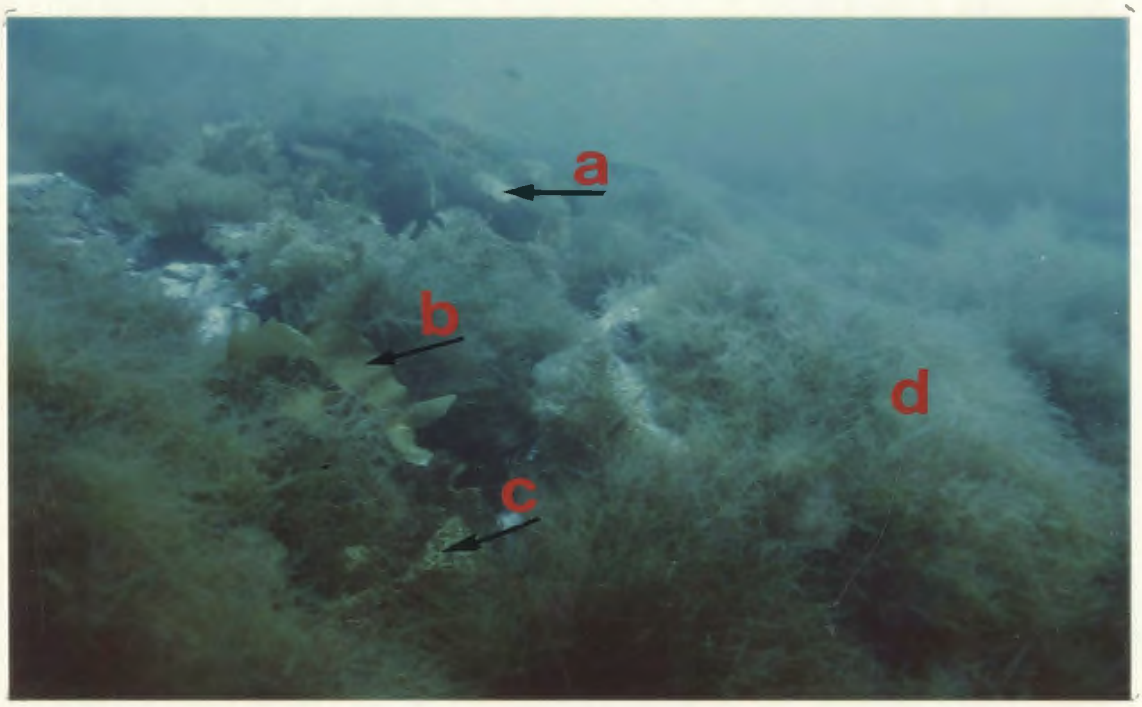

a
b
c
d

Fig. 21. Photograph illustrating the abundant *Desmarestia aculeata* in the 6-9m depth range on the quicklimed transect during the summer of 1982.

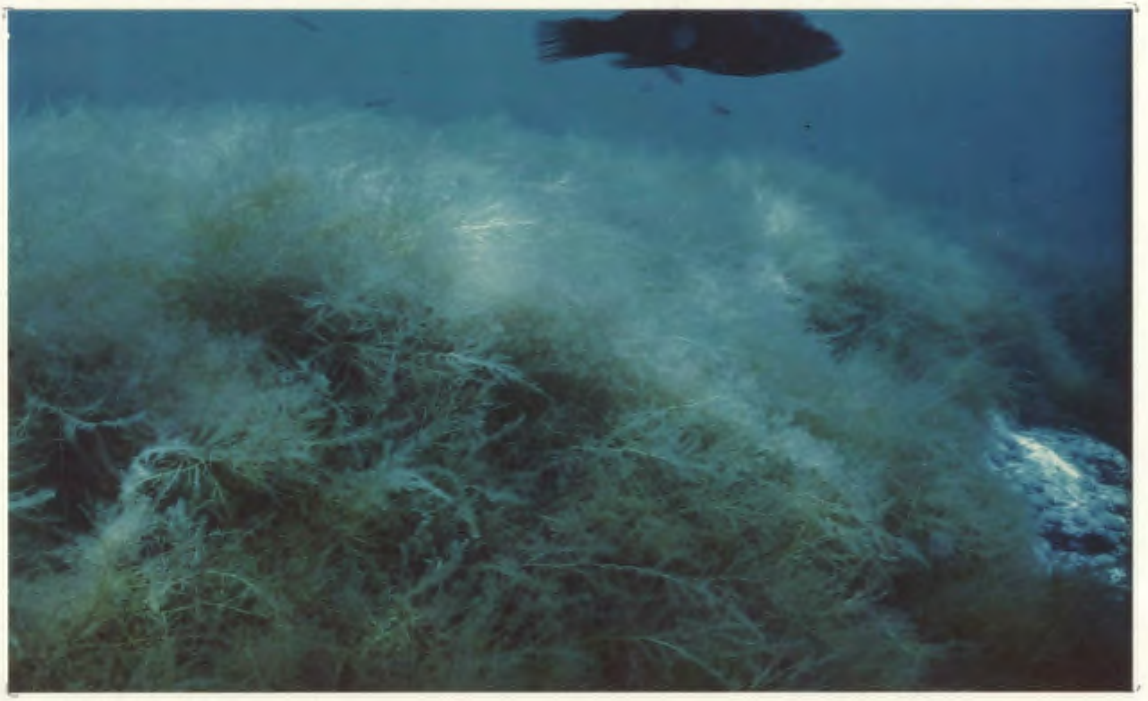


Fig. 22. Photograph illustrating a patch of *Laminaria digitata* (l) at 6-9m on the experimental transect during the summer of 1982. (d=*Desmarestia aculeata*).

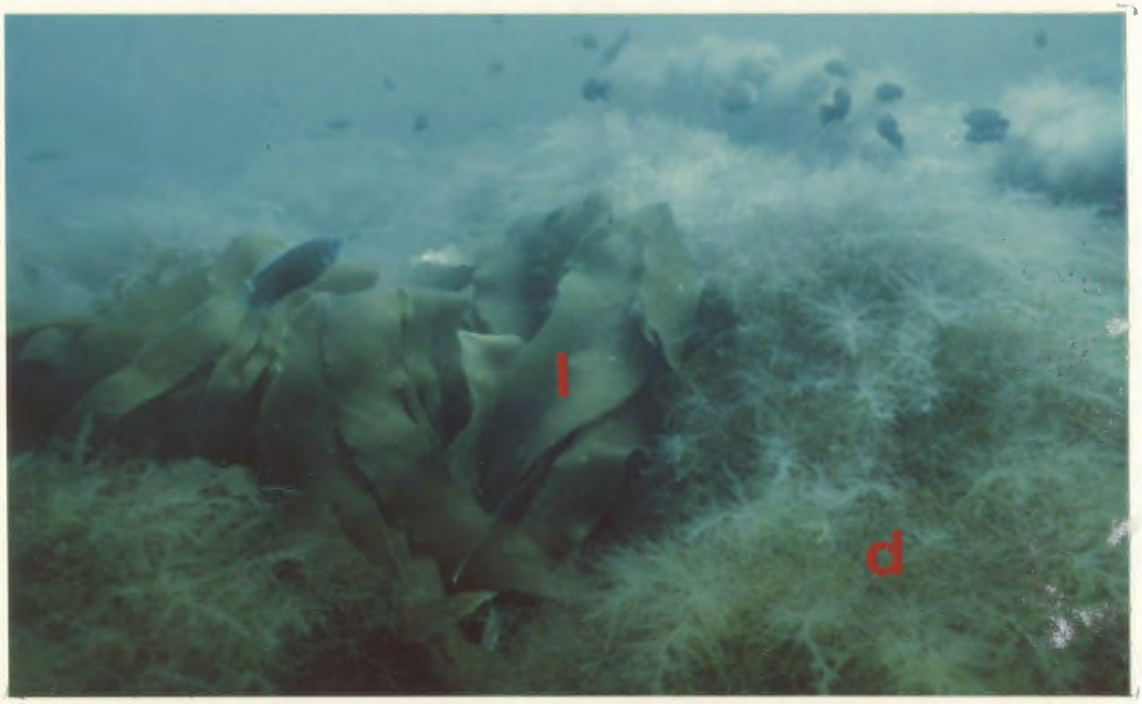

l
d

Fig. 23. Number of species of fleshy macro-algae vs. observation date for each depth and transect. Double arrows indicate time of urchin removal from the experimental transect.

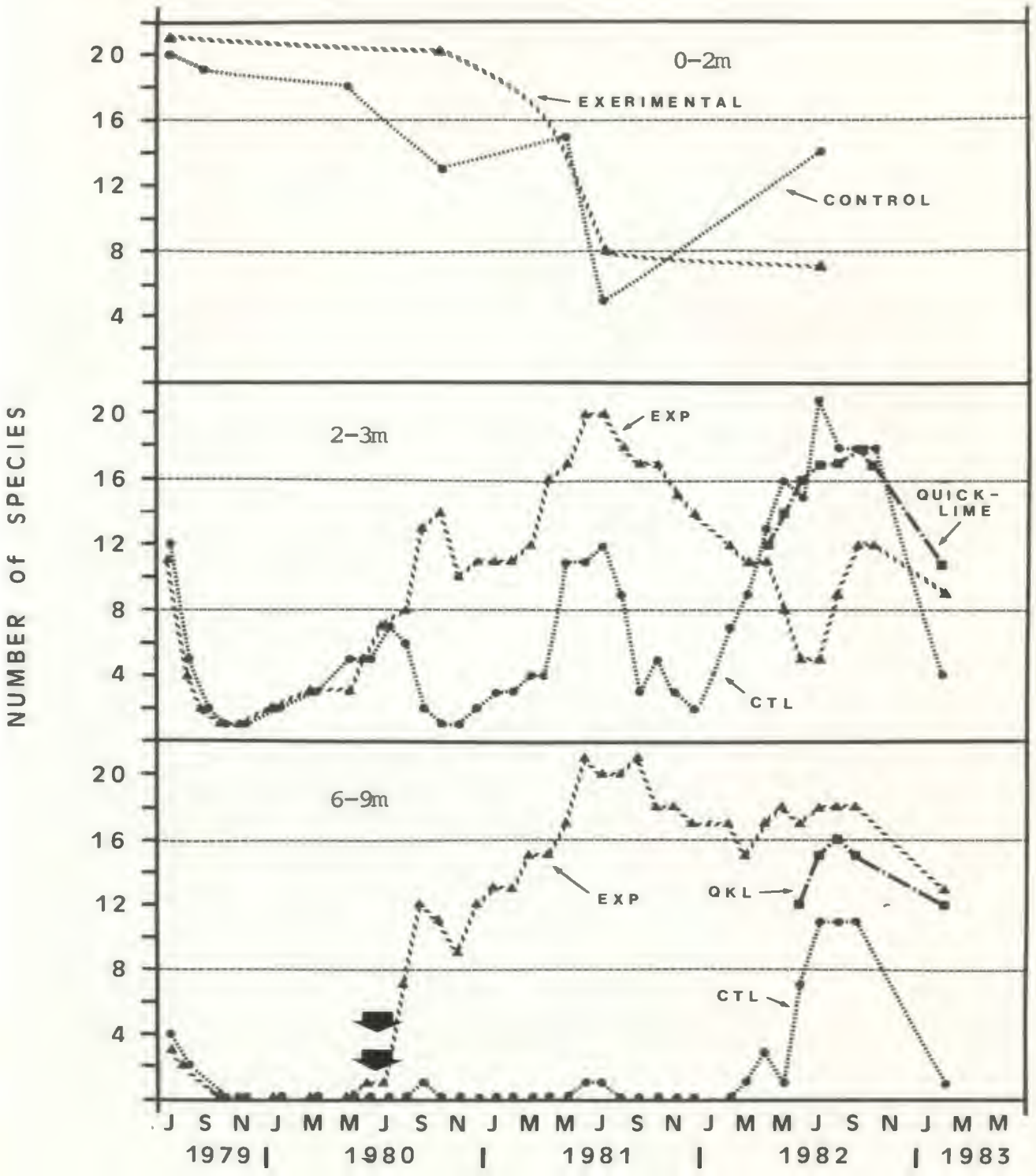

NUMBER of SPECIES
0–2m
EXERIMENTAL
CONTROL
2–3m
EXP
QUICK-
LIME
CTL
6–9m
EXP
QKL
CTL
20
16
12
8
4
J S N J M M J S N J M M J S N J M M J S N J M M
1979
1980
1981
1982
1983

Fig. 24. Dominance-diversity curves for sample sets from 0-2m for each year of the study.

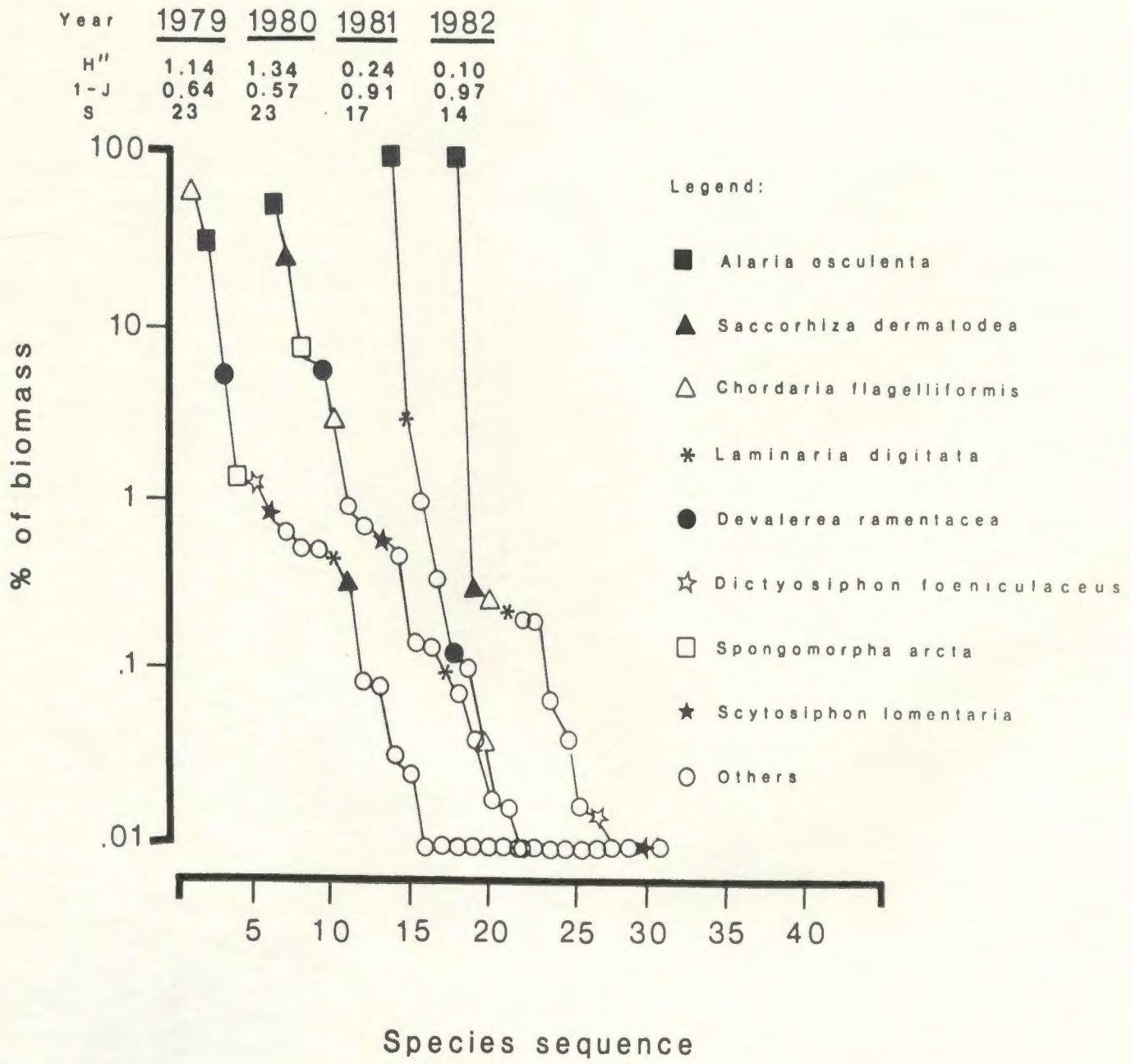

Year 1979 1980 1981 1982
H'' 1.14 1.34 0.24 0.10
1-J 0.64 0.57 0.91 0.97
S 23 23 17 14
100
10
1
.1
.01
% of biomass
5 10 15 20 25 30 35 40
Species sequence
Legend:
Alaria esculenta
Saccorhiza dermatodea
Chordaria flagelliformis
Laminaria digitata
Devalerea ramentacea
Dictyosiphon foeniculaceus
Spongomorpha arcta
Scytosiphon lomentaria
Others

Fig. 25. Photograph illustrating (a) the closed nature of the *Alaria* canopy during the spring and early summer (1982), and (b) its relatively open nature during the late summer and early autumn (1982).


a


b

Fig. 26. Dominance-diversity curves for sample sets from 2-3m, on the experimental and quicklimed transects after urchin removal. (A=Autumn 1980, experimental transect; B=Spring 1981, experimental transect; C=Spring 1982, quicklimed transect; D=Summer 1981, experimental transect; E=Summer 1982, quicklimed transect; F=Spring 1982, experimental transect; G=Summer 1982, experimental transect). Note: Curves representing the samples from the quicklimed transect are included immediately after those representing samples from the experimental transect which are approximately equivalent in term of time since urchin removal.

Urchin removal 2-3M

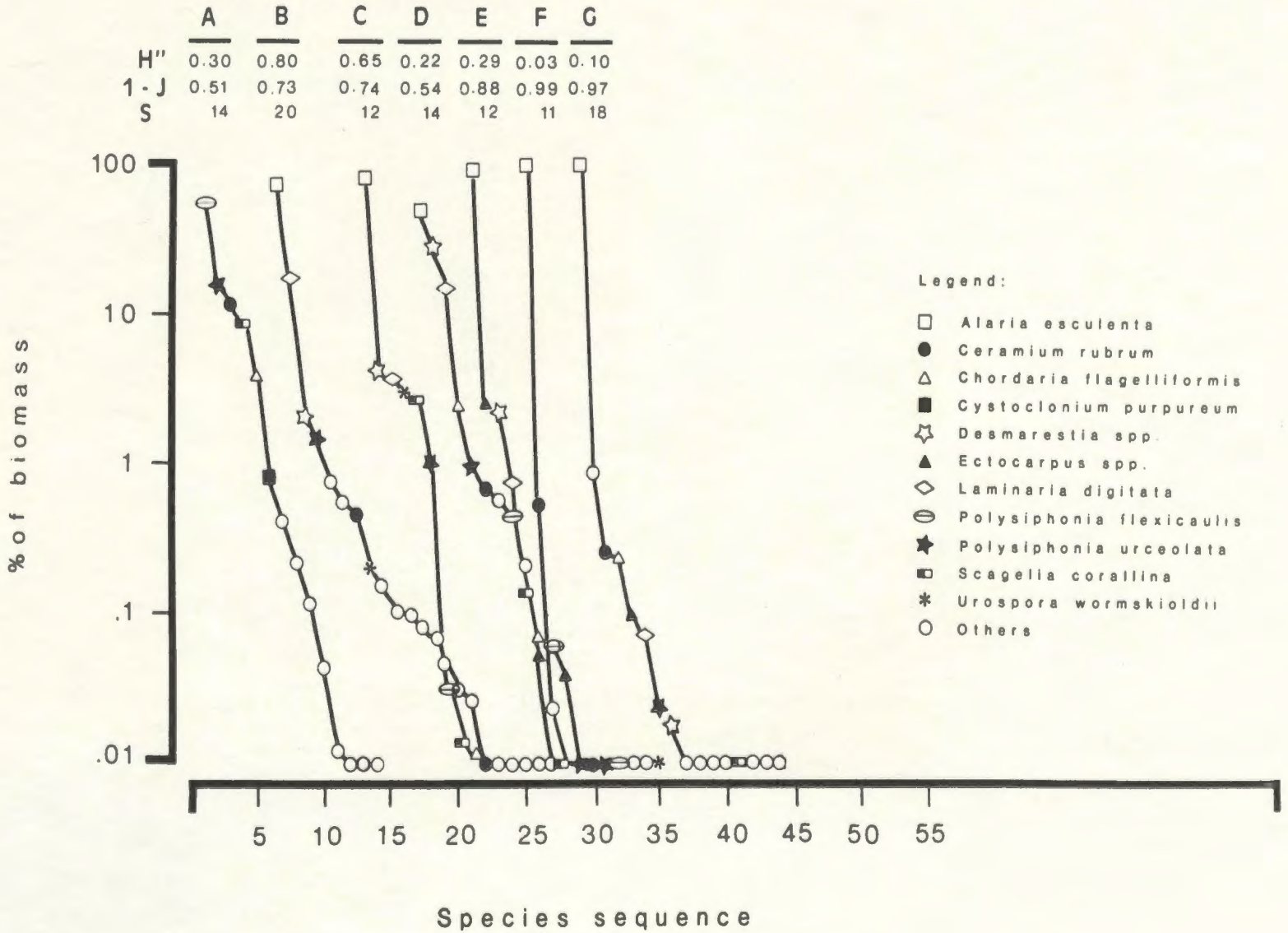


Fig. 27. Dominance-diversity curves for sample sets from 2-3m, without urchin removal. (A=Summer 1979, experimental transect before urchin removal; B=Summer 1979, control transect; C=Autumn 1979, control transect; D=Autumn 1980, control transect; E=Spring 1981, control transect; F=Summer 1981, control transect; G=Spring 1982, control transect; H=Summer 1982, control transect).

Control, 2-3M

	A	B	C	D	E	F	G	H
H"	1.09	1.28	1.26	1.80	087	0.33	2.03	1.50
1-J	0.58	0.56	0.09	0.07	069	0.88	0.03	0.52
S	13	19	4	7	16	14	8	23

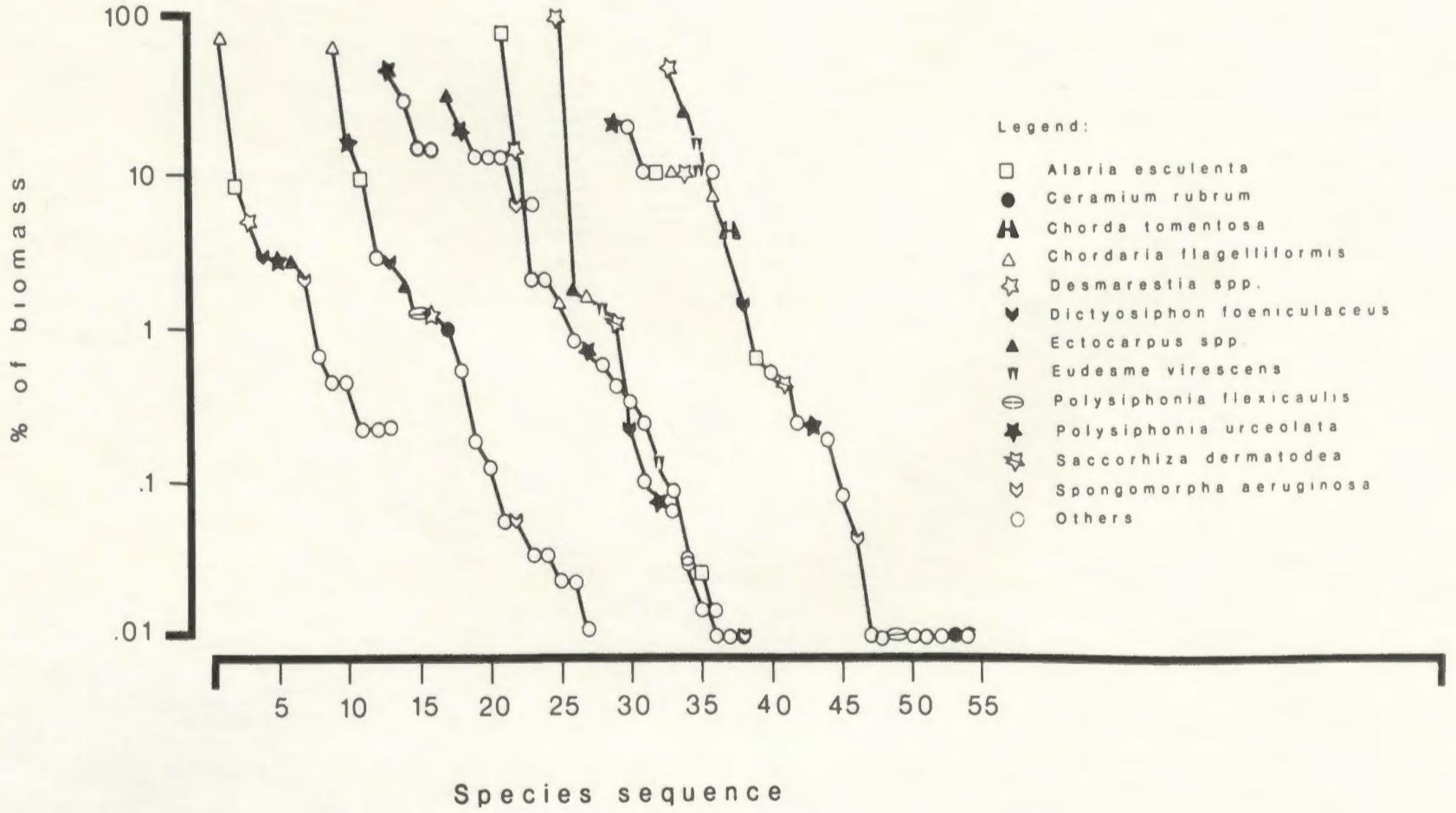


Fig. 27. Dominance-diversity curves for sample sets from 6-9m on the experimental and quicklimed transects after urchin removal. (A=Autumn 1980, experimental transect; B=Spring 1981, experimental transect; C=Summer 1981, experimental transect; D=Summer 1982, quicklimed transect; E=Spring 1982, experimental transect; F=Summer 1982, experimental transect). Note: The curves representing samples from the quicklimed transect are included immediately after those representing samples from the experimental transect which are approximately equivalent in terms of time since urchin removal.

Urchin removal 6-9M

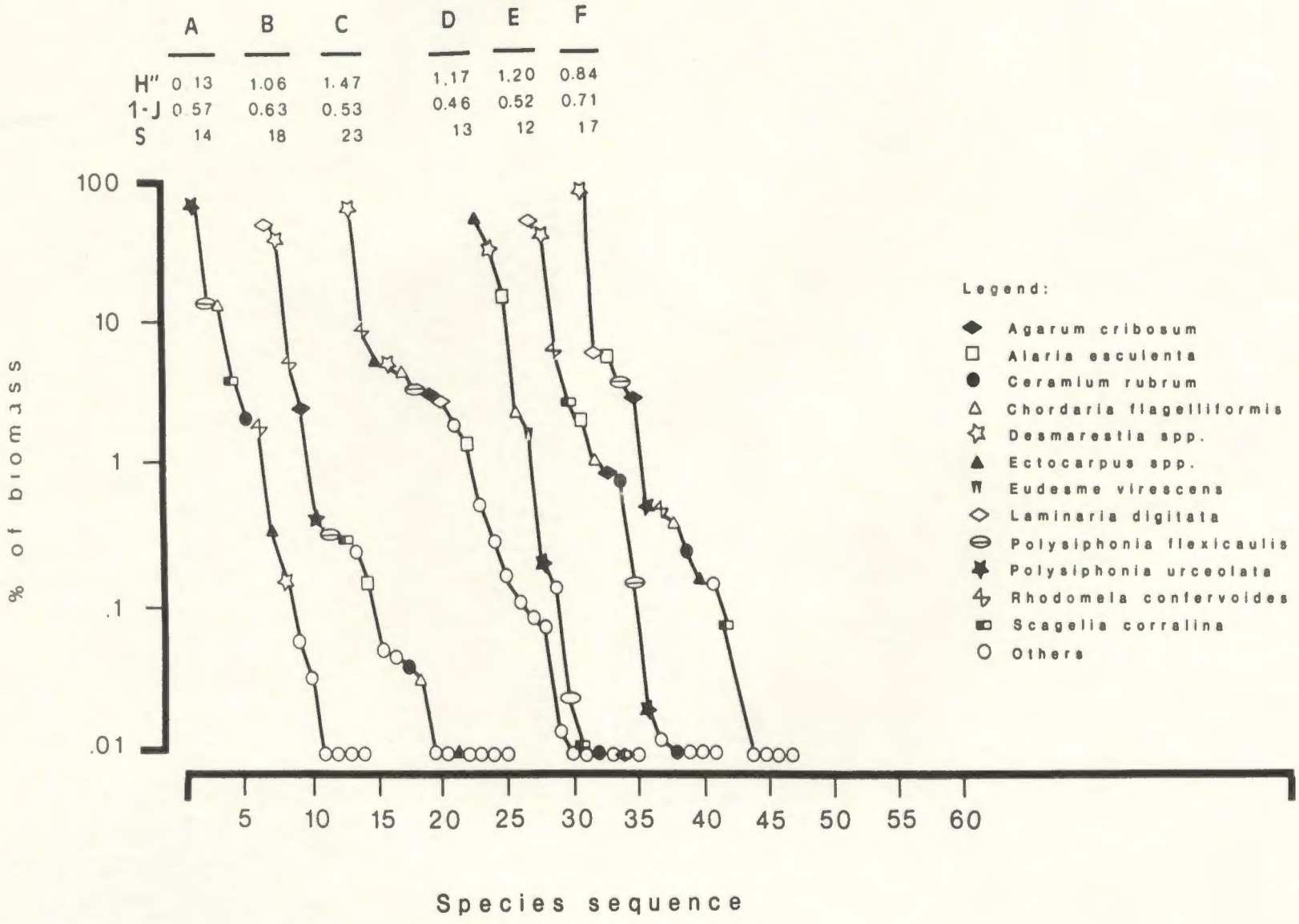


Fig. 29. Dominance-diversity curves for sample sets from 6-9m without urchin removal. (A=Summer 1979, experimental transect (before urchin removal); B=Summer 1979, control transect; C= Autumn 1979, control transect; D=Spring 1980, control transect; E=Autumn 1980, control transect; F=Spring 1981, control transect; G=Summer 1981, control transect; H=Spring 1982, control transect; I=Summer 1982, control transect).

Control, 6-9M

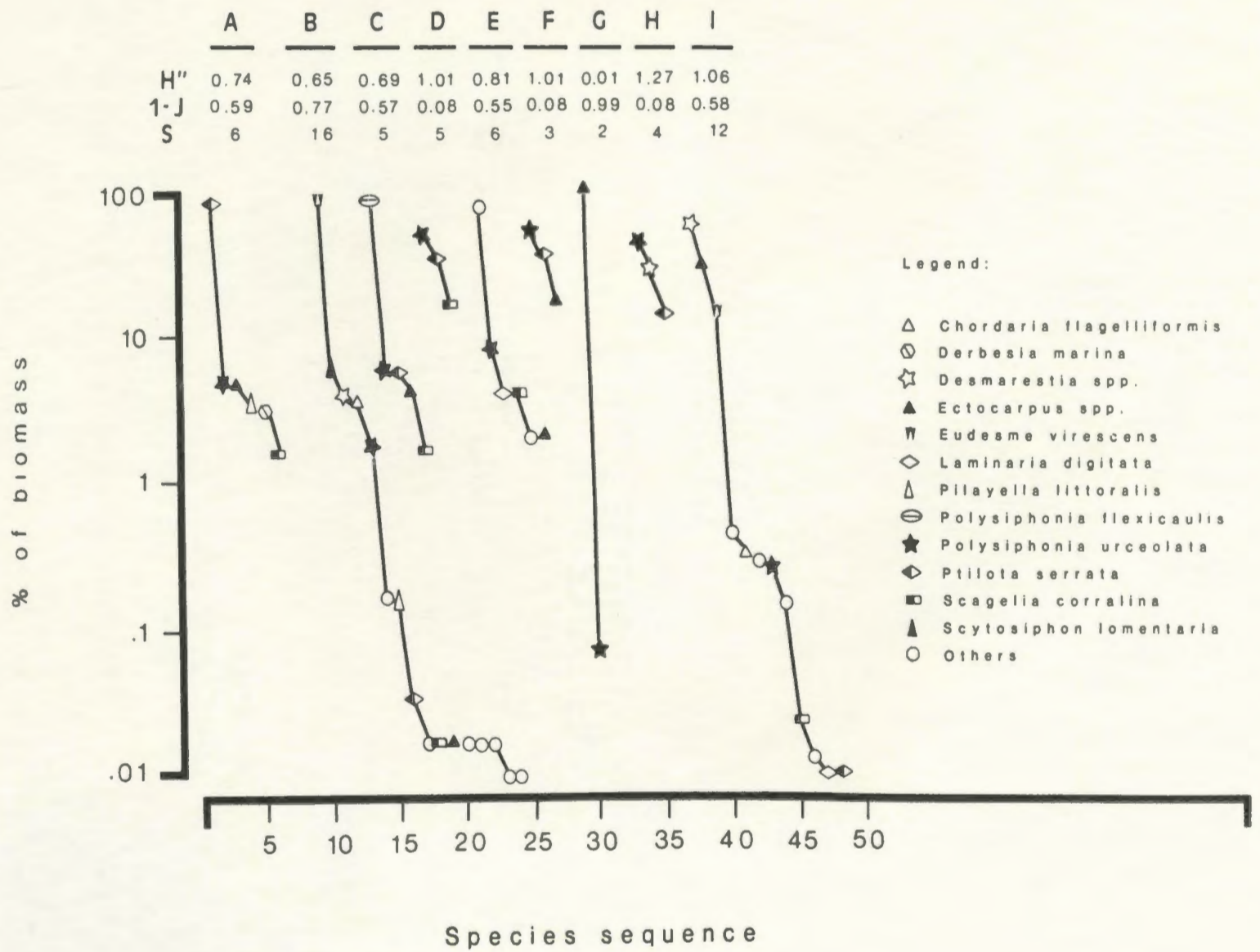

A B C D E F G H I
H" 0.74 0.65 0.69 1.01 0.81 1.01 0.01 1.27 1.06
1-J 0.59 0.77 0.57 0.08 0.55 0.08 0.99 0.08 0.58
S 6 16 5 5 6 3 2 4 12
100
10
1
.1
.01
% of biomass
5 10 15 20 25 30 35 40 45 50
Species sequence
Legend:
Chordaria flagelliformis
Derbesia marina
Desmarestia spp.
Ectocarpus spp.
Eudesme virescens
Laminaria digitata
Pilayella littoralis
Polysiphonia flexicaulis
Polysiphonia urceolata
Ptilota serrata
Scagelia corralina
Scytosiphon lomentaria
Others

Fig. 30. The number of species of annual and perennial algae from each of eight sample groupings: A= 0-2m during years in which ice-scour occurred; B= 2-3m, without urchin removal; C= 6-9m, without urchin removal; D= 2-3m, experimental transect during the autumn of 1980 (2 mo. after urchin removal); E= 6-9m, experimental transect during the autumn of 1980 (2 mo. after urchin removal); F= 0-2m, during years in which no ice-scour occurred; G= 2-3m, removal areas (experimental + quicklimed transects) more than 9 mo. after urchin removal; H= 6-9m, removal areas more than 9 mo. after urchin removal. Note: Species recorded only as present (< 0.05 g m^{-2}) are included in these data.

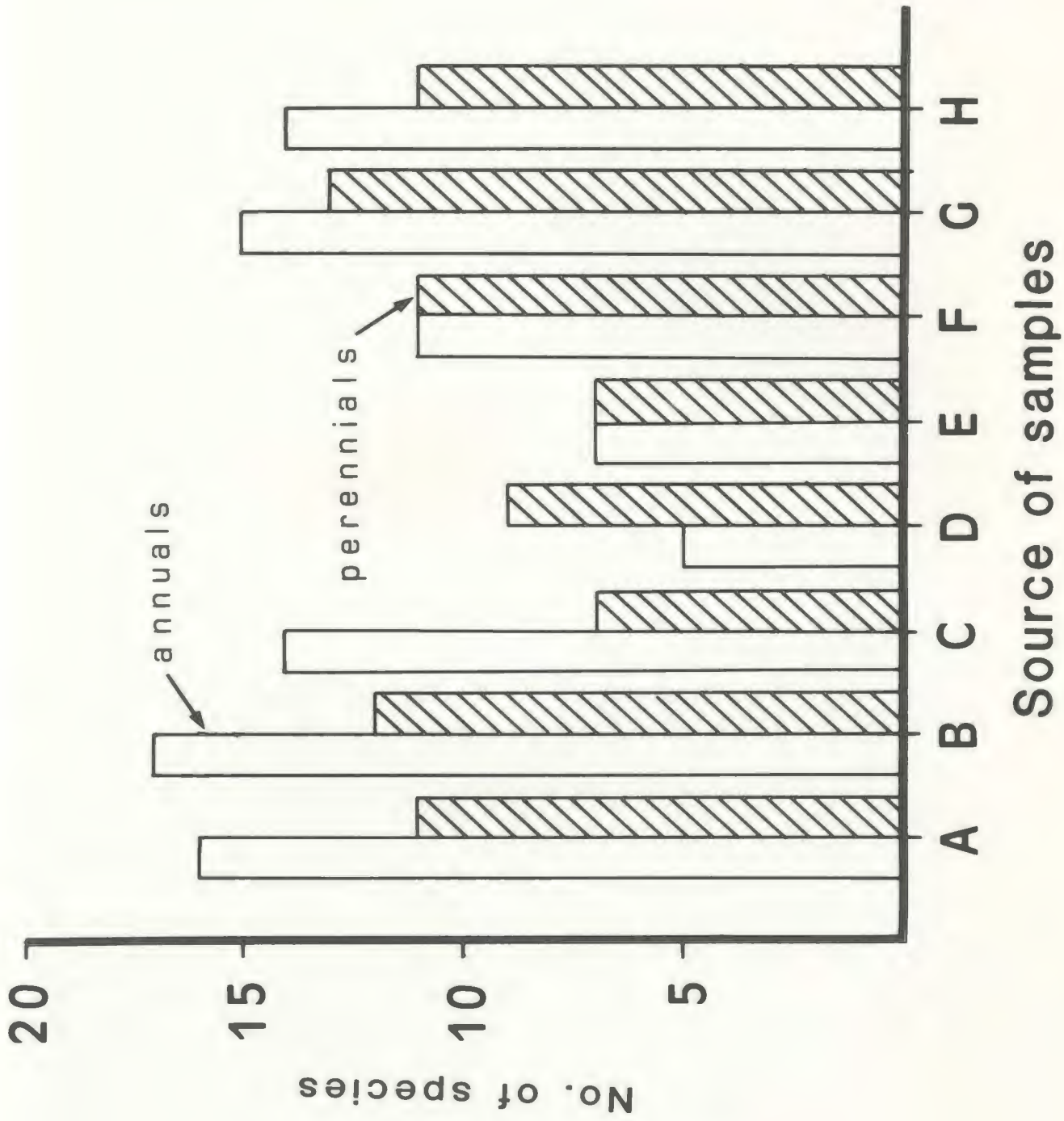

20
15
10
5
No. of species
annuals
perennials
A
B
C
D
E
F
G
H
Source of samples

Fig. 31. The number of species of annual and perennial algae from each of eight sample groupings: A= 0-2m during years in which ice-scour occurred; B= 2-3m, without urchin removal; C= 6-9m, without urchin removal; D= 2-3m, experimental transect during the autumn of 1980 (2 mo. after urchin removal); E= 6-9m, during the autumn of 1980 (2 mo. after urchin removal); F= 0-2m, during years in which no ice-scour occurred; G= 2-3m, removal areas (experimental & quicklimed transects), more than 9 mo. after urchin removal; H=6-9m, removal areas, morethan 9 mo, after urchin removal. Note: Species recorded only as present (<0.05 g m^{-2}) are excluded from these data.

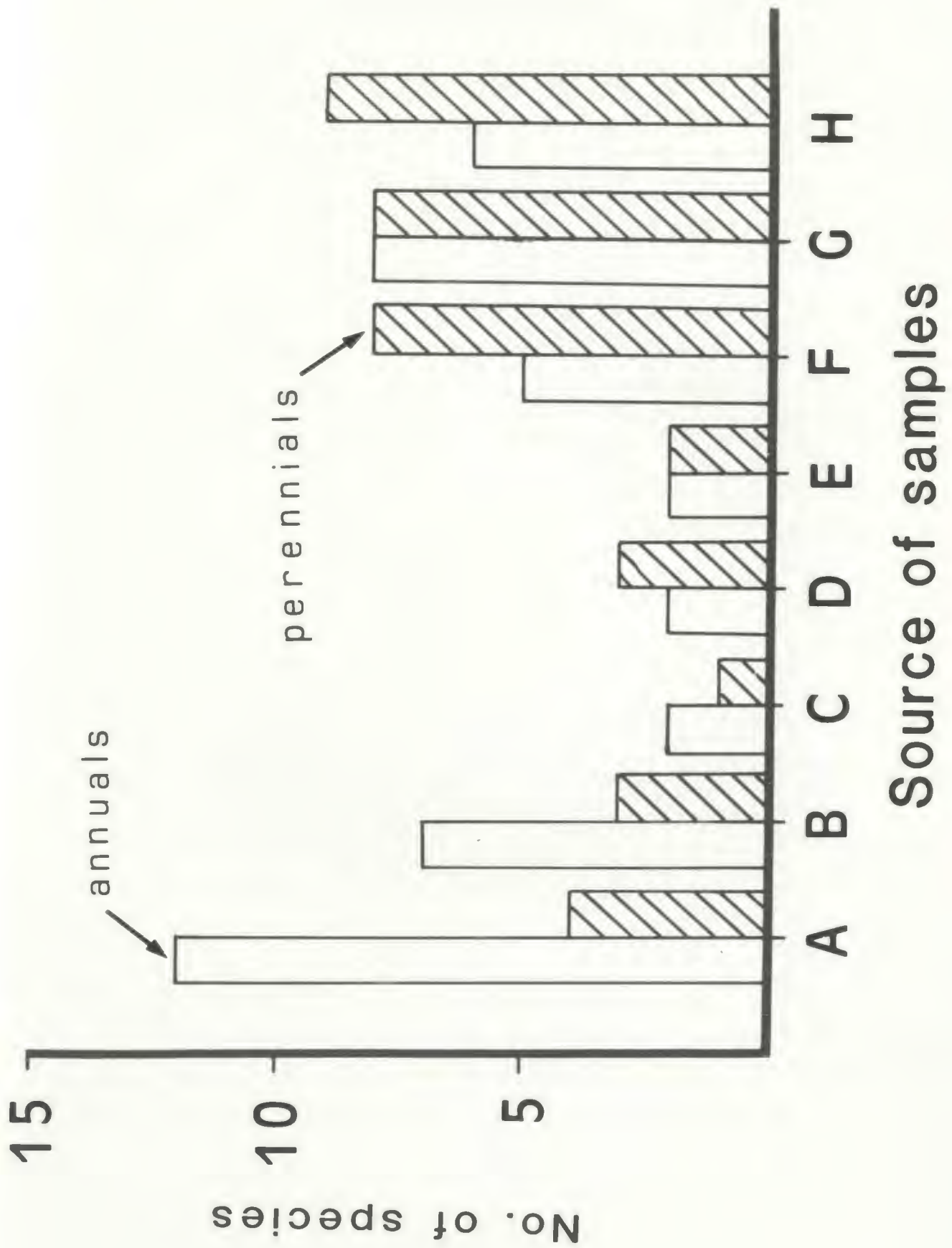

15
10
5
No. of species
annuals
perennials
A
B
C
D
E
F
G
H
Source of samples

Fig. 32. Percentage of biomass for annual and perennial algae from each of eight sample groupings: A= 0-2m during years in which ice-scour occurred; B= 2-3m, without urchin removal; C= 6-9m without urchin removal; D= 2-3m, experimental transect during the autumn of 1980 (2 mo. after urchin removal); E= 6-9m, experimental transect during the autumn of 1980 (2 mo. after urchin removal); F= 0-2m during years in which no ice-scour occurred; G= 2-3m, removal areas, more than 9 mo. after urchin removal; H= 6-9m, removal areas more than 9 mo. after urchin removal.

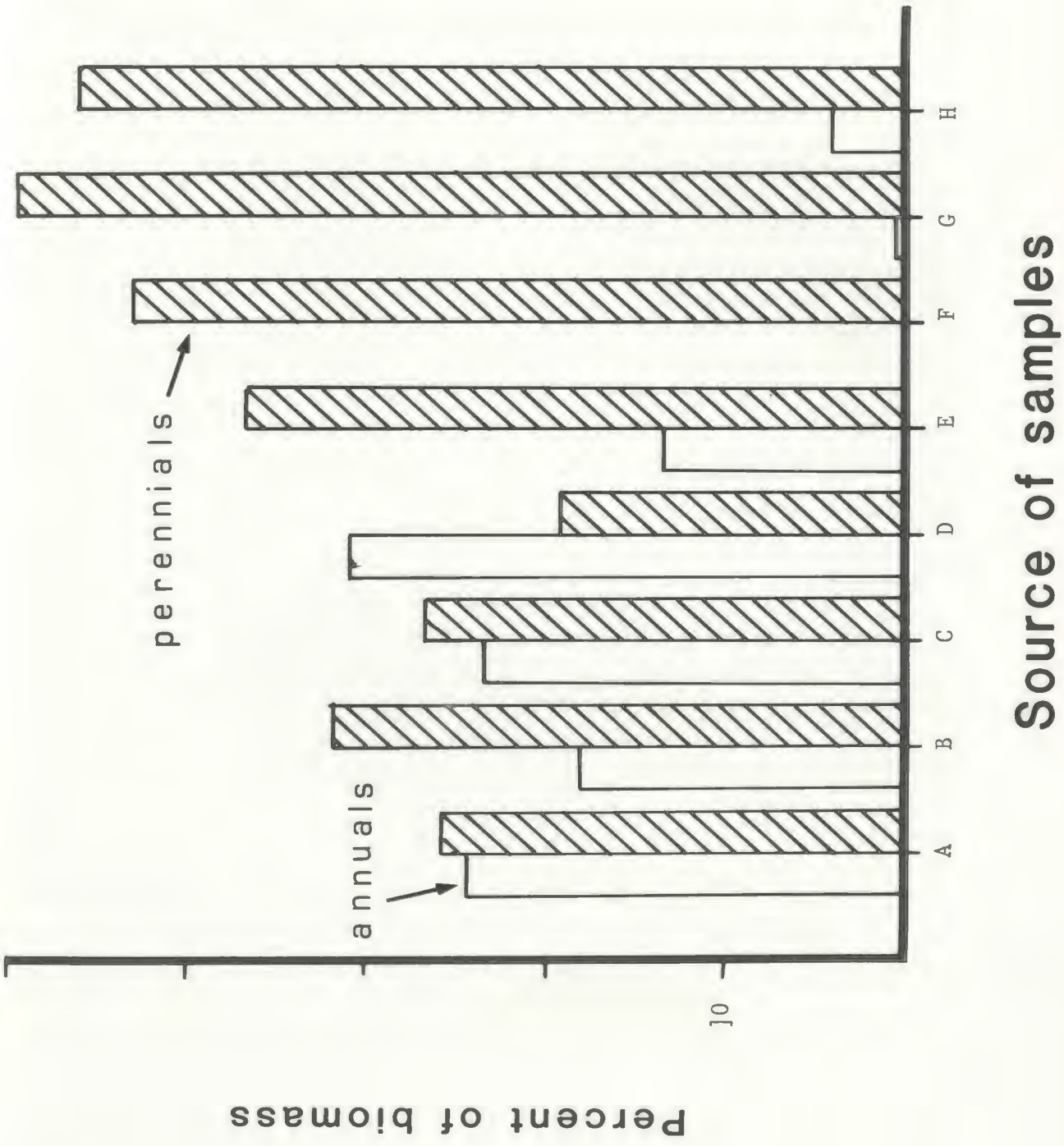

Percent of biomass
10
annuals
perennials
A
B
C
D
E
F
G
H
Source of samples

Fig. 33. Urchin biomass for each transect, depth, and sample date [geometric mean (g m^{-2}) $\pm$ std. err.].

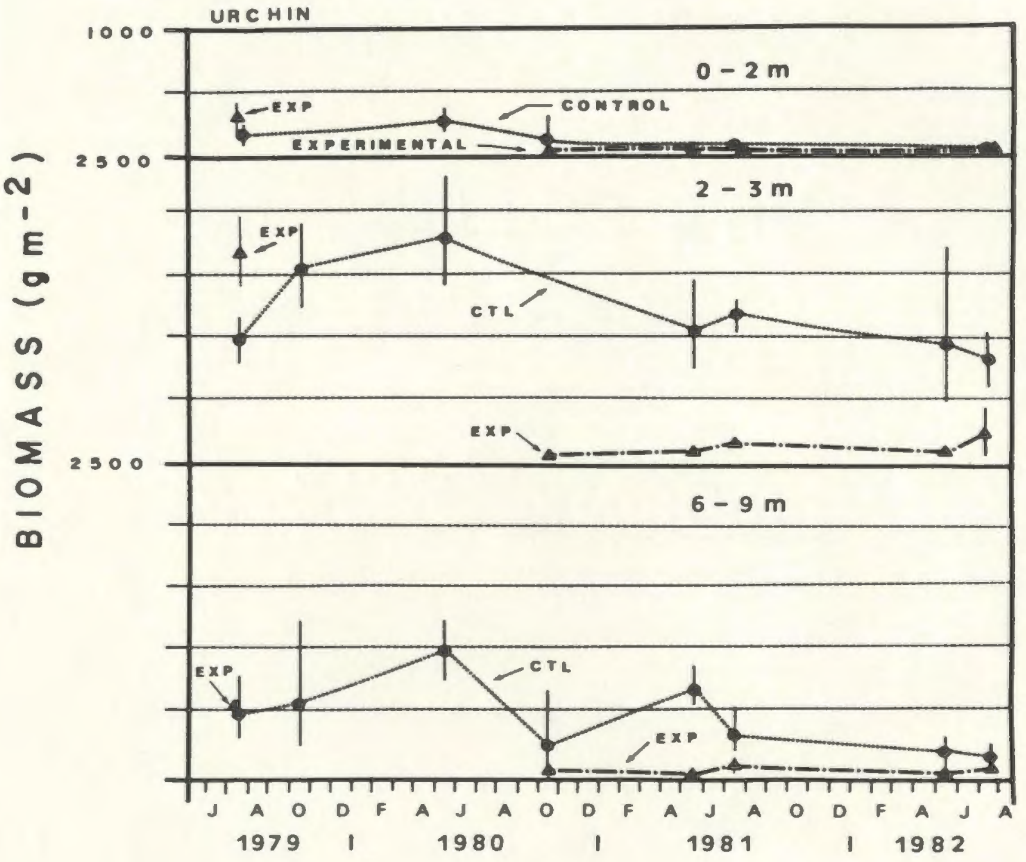

URCHIN
1000
2500
2500
BIOMASS (g m-2)
0 - 2 m
EXP
CONTROL
EXPERIMENTAL
2 - 3 m
EXP
CTL
EXP
6 - 9 m
EXP
CTL
EXP
J A O D F A J A O D F A J A O D F A J A
1979 1980 1981 1982

Fig. 34. Urchin size frequency distributions from 0-2m. Note: The curves for 1979 are based on 5 mm size ranges; other curves are based on 2 mm size ranges. (C=Control transect, E=Experimental transect).

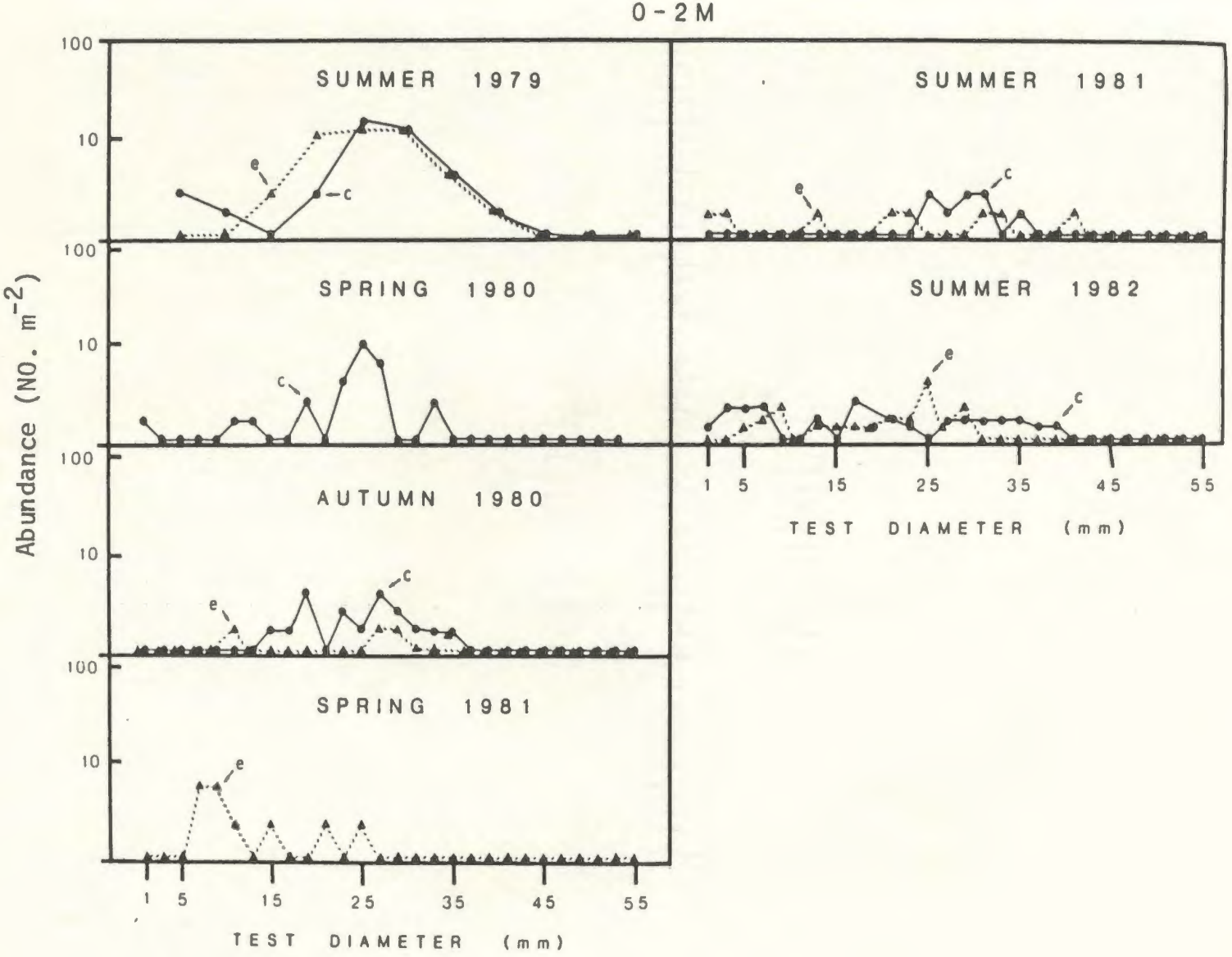

0-2M
SUMMER 1979
SUMMER 1981
SPRING 1980
SUMMER 1982
AUTUMN 1980
SPRING 1981
100
10
e
c
Abundance (NO. m-2)
1 5 15 25 35 45 55
TEST DIAMETER (mm)

Fig. 35. Urchin size frequency distributions from 2-3m. Note: The curves from summer 1979 are based on 5 mm size ranges, all others on 2 mm size ranges. (C=Control transect; E=Experimental transect; Q=Quicklimed transect).

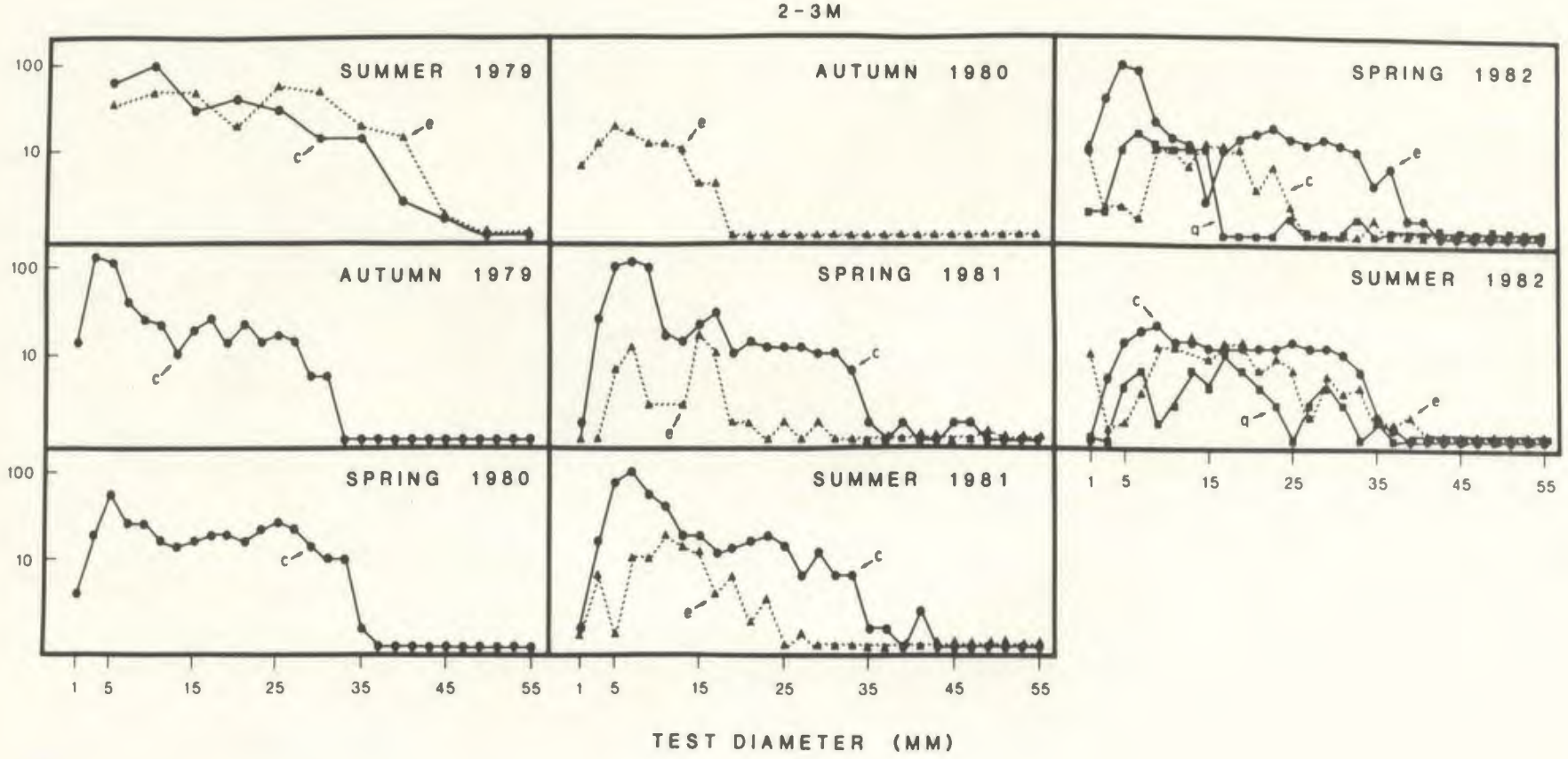

2-3M
SUMMER 1979
AUTUMN 1980
SPRING 1982
AUTUMN 1979
SPRING 1981
SUMMER 1982
SPRING 1980
SUMMER 1981
c
e
q
100
10
1
5
15
25
35
45
55
ABUNDANCE (NO.·M⁻²)
TEST DIAMETER (MM)

Fig. 36. Urchin size frequency distributions from 6-9m. Note: the curves from 1979 are based on 5 mm size ranges, all others on 2 mm size ranges. (C=Control transect; E=Experimental transect; Q=Quicklimed transect).

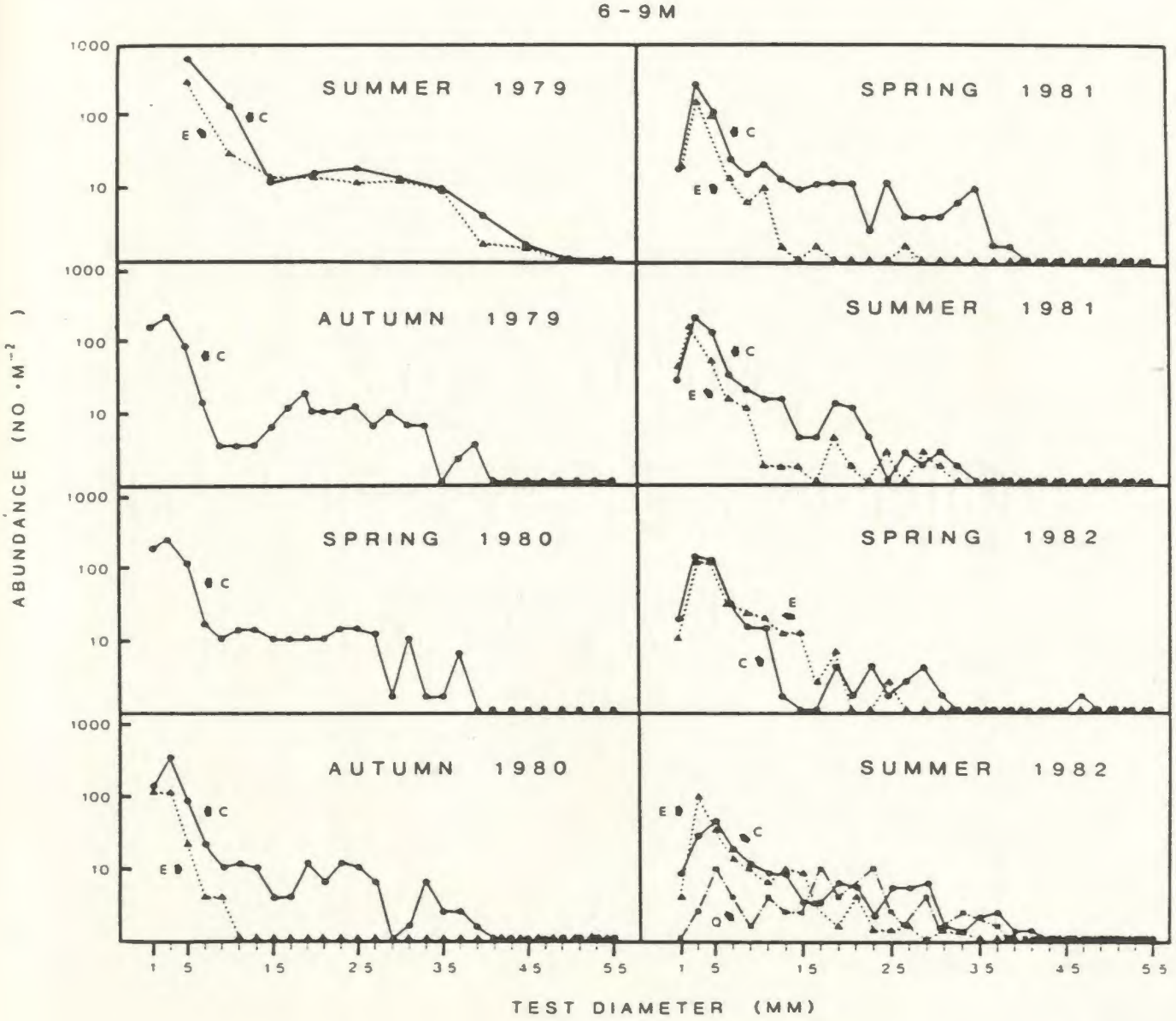

6-9M
SUMMER 1979
SPRING 1981
AUTUMN 1979
SUMMER 1981
SPRING 1980
SPRING 1982
AUTUMN 1980
SUMMER 1982
C
E
Q
1000
100
10
1
5
15
25
35
45
55
ABUNDANCE (NO·M⁻²)
TEST DIAMETER (MM)

Fig. 37. Urchin size frequency distributions from 12-18m. Note: all curves are based on 2mm size ranges (C=Control transect).

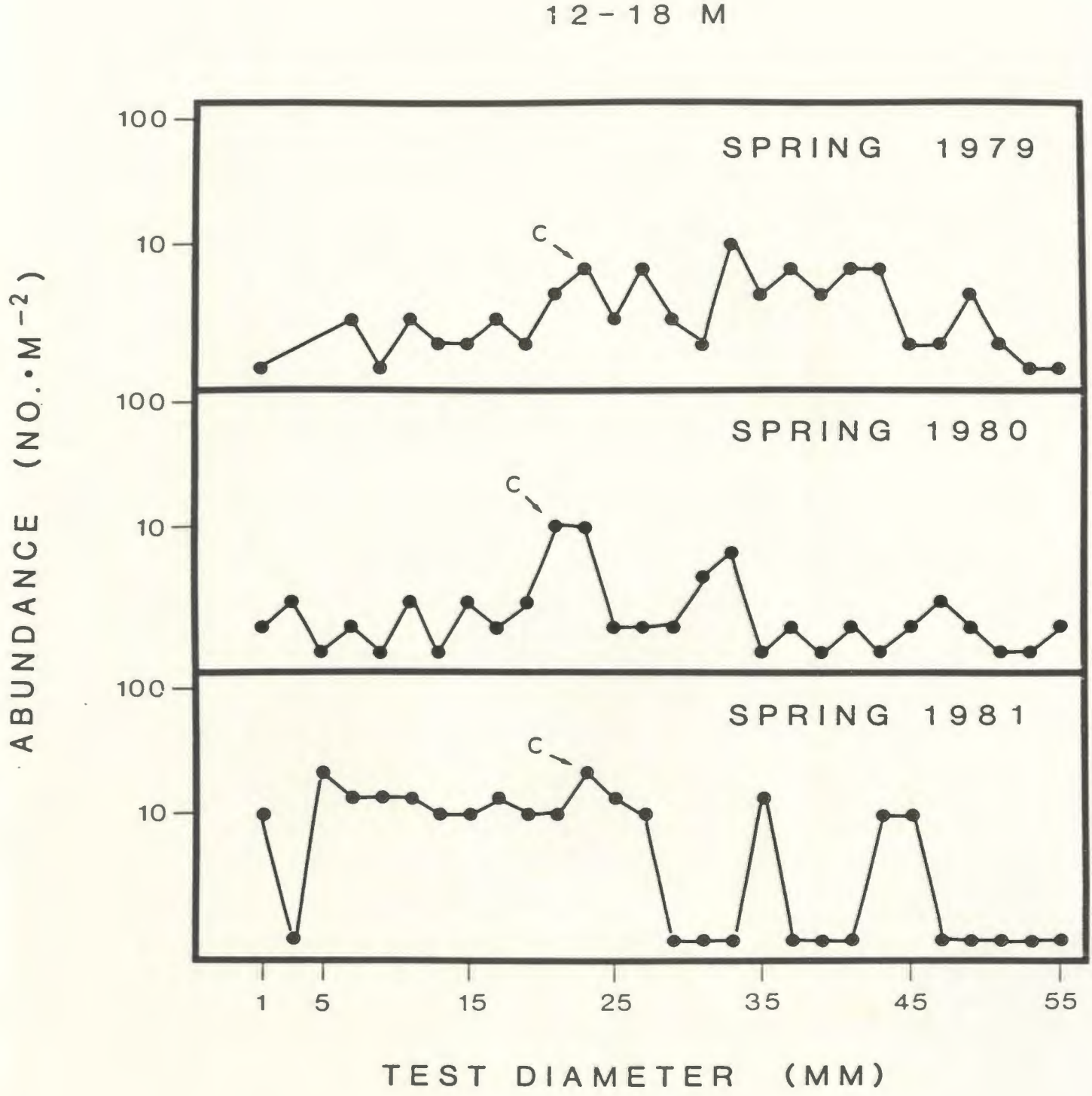

12-18 M
SPRING 1979
SPRING 1980
SPRING 1981
C
100
10
ABUNDANCE (NO.·M⁻²)
1
5
15
25
35
45
55
TEST DIAMETER (MM)

Fig. 38. Juvenile *Alaria esculenta* showing damage from browsing by *Lacuna vincta*.

Fig. 39. Schematic representation of the known and hypothesized effect of ice-scour on shallow water, open coast communities in eastern Newfoundland. (See text for explanation).

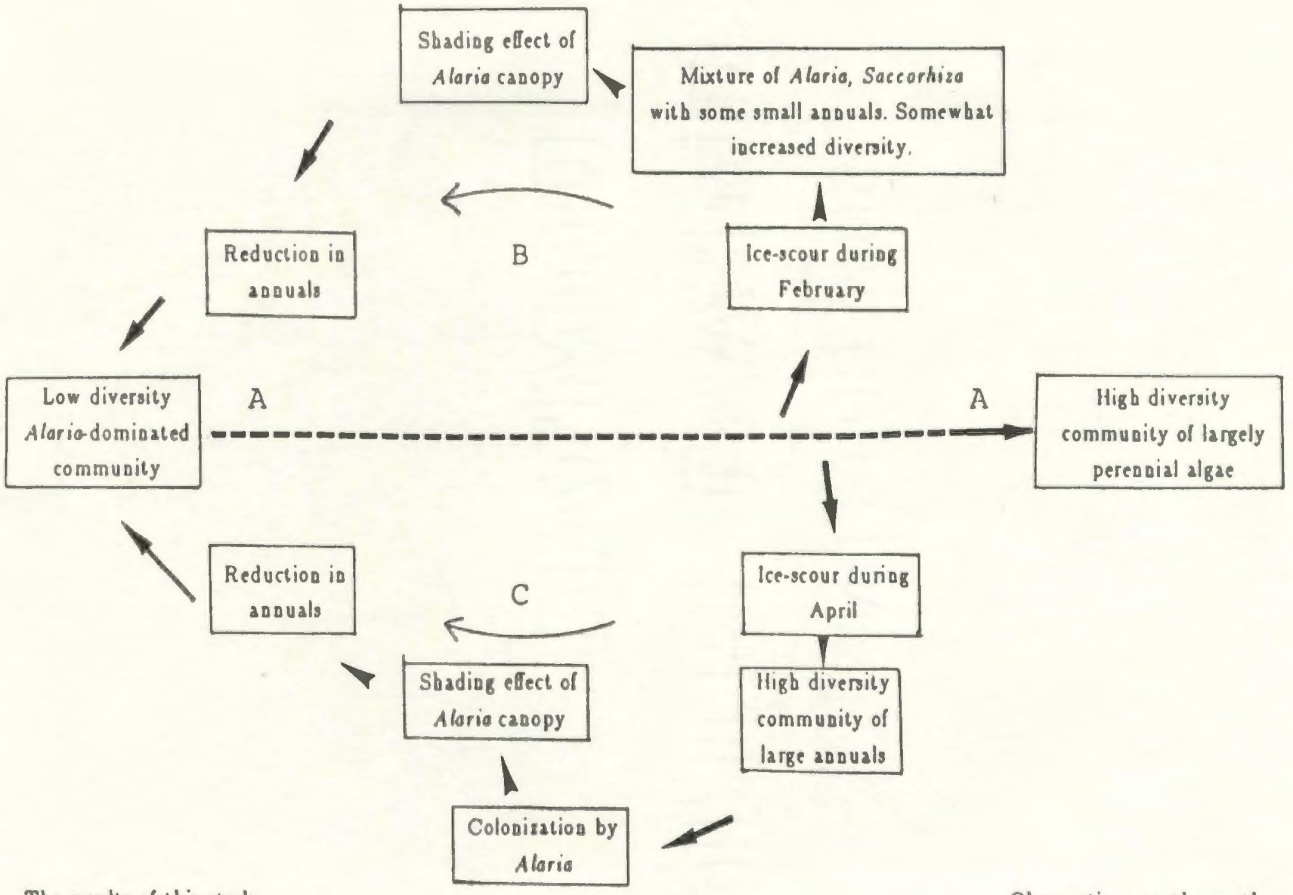

Shading effect of *Alaria* canopy
Mixture of *Alaria*, *Saccorhiza* with some small annuals. Somewhat increased diversity.
Reduction in annuals
B
Ice-scour during February
Low diversity *Alaria*-dominated community
A
A
High diversity community of largely perennial algae
Reduction in annuals
C
Ice-scour during April
Shading effect of *Alaria* canopy
High diversity community of large annuals
Colonization by *Alaria*
The results of this study
Observations on the south coast

Table 1. Summary of the field work undertaken during the course of the present study.

Study areas selected;transect lines established preliminary sampling to determine quadrat size, number & logistic requirements	Apr. - June 1979
Pre-treatment sampling of transects; Monthly observations and species counts	July - Aug. 1979
Determine the feasibility of autumn sampling; Monthly observations and species counts	Sept. - Oct. 1979
Monthly observations and species counts	Nov. 79 Apr. 1980
Sample control transect; Monthly observations and species counts; preparations for manual urchin removal	May 1980
Manual urchin removal; Monthly observations and species counts	June - Aug. 1980
Sample control and experimental transects; Monthly observations and species counts	Sept. - Oct. 1980
Monthly observations and species counts	Nov. 1980 - Apr. 1981
Sample control and experimental transects Monthly observations and species counts	May 1981
Locate and survey area for, and conduct a trial quicklime application to determine dosage and technique; monthly observations and species cts	June 1981
Sample control and experimental transects; Monthly observations and species counts	July 1981
Monthly observations and species counts	Aug. - Sept. 1981
Monthly observations and species counts; Quickliming	Oct. - Nov. 1981
Monthly observations and species counts conducted thereafter until February, 1983. Sampling conducted on the control, experimental and quicklime transects during May and July,1982	

Table 2. Summary of the sampling data obtained during the urchin removal experiment (Number in parentheses is the number of samples.

	SUMMER 1979		AUTUMN 1979		SPRING 1980		AUTUMN 1980		SPRING 1981		SUMMER 1981		SPRING 1982			SUMMER 1982		
TRANSECT:	C	E	C	E	C	E	C	E	C	E	C	E	C	E	Q	C	E	Q
SAMPLE DEPTH RANGE																		
0-2M	(5)	(5)	-	-	(5)	-	(4)	(5)	-	(3)	(5)	(5)	-	-	-	(10)	(10)	-
2-3M	(5)	(5)	(3)	-	(5)	-	-	(5)	(5)	(5)	(5)	(6)	(5)	(6)	(5)	(10)	(10)	(5)
6-9M	(5)	(5)	(4)	-	(5)	-	(5)	(5)	(5)	(5)	(5)	(5)	(5)	(5)	-	(10)	(10)	(5)

E=Experimental transect, C=Control transect, Q=Quicklimed transect.

Table 3. List of taxa used in the cluster analysis, the frequency of their occurrence in the 43 transect, depth and sample period combinations, and whether they were considered annual or perennial.

Taxon	Frequency of Occurrence	Annual(A) or Perennial(P)
Acrothrix novae-angliae Taylor	2	A
Agarum cribrosum (Mert.) Bory	7	P
Alaria esculenta (L.) Grev.	28	P
Antithamnionella floccosa (O. F. Müll.) Whittick	8	A
Callophyllis cristata (C. Ag.) Kütz.	5	P
Ceramium rubrum (Huds.) C. Ag.	21	P
Chorda tomentosa Lyngb.	7	A
Chordaria flagelliformis (O.F. Müll.) C. Ag.	27	A
Derbesia marina (Lyngb.) Solier	8	A
Desmarestia spp.*	23	P**
Devaleraea ramentacea (L.) Guiry	18	A
Dictyosiphon foeniculaceus (Huds.) Grev.	13	A
Ectocarpus spp.***	32	A
Eudesme virescens (Carm. ex Harv. in Hook) J.Ag.	10	A
Giffordia sp.	9	A
Laminaria digitata (Huds.) Lamour.	23	P
Membranoptera alata (Huds.) Stackh.	3	P
Monostroma grevilleii (Thur.) Wittr.	2	A
Palmaria palmata (L.) O. Kuntze	9	P
Petalonia fascia (O.F. Müll.) O. Kuntze	19	A
Petalonia zosterifolia (Reinke) O. Kuntze	3	A
Phycodrys rubens (l.) Batt.	5	P
Pilayella littoralis (L.) Kjellm.	17	A
Polysiphonia flexicaulis (Harv.) Coll.	19	A
Polysiphonia urceolata (Lightf. ex Dillw.) Grev.	43	P
Ptilota serrata Kütz.	28	P
Punctaria plantaginea (Roth) Grev.	2	A
Rhodomela confervoides (Huds.) Silva	17	P
Saccorhiza dermatodea (Pyl.) J. Ag.	12	A
Scagelia pylaisaei (Mont.) Wynne	*36*	*P*
Scytosiphon lomentaria (Lyngb.) Link	12	A
Spongomorpha aeruginosa (L.) Hoek	14	A
Spongomorpha arcta (Dillw.) Kütz.	17	A
Urospora wormskjoldii (Mert. in Hornem.) Rosenv.	3	A

Desmarestia aculeata* (L.) Lamour. and *D. viridis* (O. F. Müll.) Lamour. ***D. aculeata* is perennial, and *D. viridis* is annual. Only pooled biomass data for both species is available, and because *D. aculeata* was the more abundant species, *Desmarestia* spp. has been assigned perennial status. * *Ectocarpus fasiculatus* Harv. and *E. siliculosus* (Dillw.) Lyngb.

Table 4. Species presece/absence from observations made monthly throughout the study at 2-3m.

SPECIES		1979 JASOND	1980 JFMAMJJASOND	1981 JFMAMJJASOND	1982 JFMAMJJASO..F
Acrothrix novaeangliae	C	+-----	-----++-----	-----++-----	----++--- -
	E	+-----	-----++++--	-----++++--	---------- -
	Q				------- -
Alaria esculenta	C	+-----	----------+	++++++++++	-+++++++++ -
	E	+-----	----------+	++++++++++	++++++++++ +
	Q				+++++++ +
Chorda tomentosa	C	------	----------	----------	----++--- -
	E	------	----------	---++++---	---+------ -
	Q				--+---- -
Chordaria flagelliformis	C	+-----	-----++-----	----++++--	----++++++ -
	E	+-----	-----++-----	----++++--	----++++++ -
	Q				--++++++ +
Desmarestia aculeata	C	++++++	++++++++++	++++++++++	++++++++++ +
	E	++++++	++++++++++	++++++++++	+++------- -
	Q				+++++++ +
Desmarestia viridis	C	+++---	++++++++---	++++++++--	++++++++++ +
	E	+++---	++++++++--+	++++++++--	++--------- -
	Q				+++++++ -
Dictyosiphon foenlculaceus	C	+-----	------+-----	------+----	----------+++ -
	E	+-----	------++++-	-----++----	---------- -
	Q				---++++ -
Ectocarpus spp.	C	++----	----+-------	---++++---	---++++++ -
	E	++----	-------++++	+---++++++	---------++ -
	Q				-++++++ -
Eudesme virescens	C	+-----	-----++-----	-----++----	----------+++ -
	E	+-----	-----++++--	-----++++++	---------- -
	Q				--+++-- -
Giffordia sp.	C	------	----------	----+------	---------- -
	E	------	----------+----		---------- -
	Q				-++----- -
Laminaria digitata	C	------	----------	----++----	--++++++++ -
	E	------	----------++++	++++++++++	++++++++++ +
	Q				+++++++ +
Petalonia fascia	C	------	----------	-----++----	------+++ +
	E	------	----------	-----++++--	---------- -
	Q				+------ -

Table 4, continued.

Pilayella littoralis	C	+----- -----+----- ----++---- ---++++++	-
	E	+----- -----++++- ----+++++++ ---++++++	-
	Q	++++++	-
Saccorhiza dermatodea	C	------ ---------- ----++++-- ------+++	-
	E	------ ---------- ---+++++++ +++------	-
	Q	+++++++	+
Scytosiphon lomentaria	C	------ ---------- ----++++-- ------+++	+
	E	------ ---------- ----++++--- ----------	-
	Q	-------	-
Tilopteris mertensii	C	------ ---------- ---------- ------+--	-
	E	------ ---------- ---+------- ---+------	-
	Q	-------	-
Antithamnion pylaisaei	C	------ ---------- ---------- -+++++++++	-
	E	------ --------++++ ++++++++++ ++++++++++	+
	Q	+++++++	+
Antithamnionella floccosa	C	+----- +++------- ---------- -++++---++	-
	E	+----- -++++----- -++++----++ ++++----++	+
	Q	+++++++	+
Bangia atropurpurea	C	------ ---------- --+------- ----------	-
	E	------ ---------- --+++----- ----------	-
	Q	-------	-
Ceramium rubrum	C	++---- ---------- ---------- ++++++++++	-
	E	------ ---------+++ +++++++--+++ ++++++-+++	+
	Q	++-++++	+
Gloiosiphonia capillaris	C	------ ---------- ---------- ----------	-
	E	------ ---------- ---------- ---------++	-
	Q	------++	-
Cystoclonium purpureum	C	------ ---------- -------+--- ----------	-
	E	------ ---------- ---------- ----------	-
	Q	-------	-
Halosaccion ramentaceum	C	------ ---------- ----+++--- ----------	-
	E	------ ---------- ---------- ----------	-
	Q	-------	-
Palmaria palmata	C	------ ---------- ---------- ----------	-
	E	------ ---------- ---------- ----------	-
	Q	--+++++	+
Polysiphonia flexicaulis	C	------ ---------- ---------++- ---------++	-
	E	------ --------++++ ++++++++++ +++------++	+
	Q	---++++	+

Table 4, continued.

Polysiphonia urceolata	C	++-----	----------	---------++--	---------++	-
	E	++-----	--------+++	+++++++++++	++++++++++	+
	Q				+++++++	+
Porphyra sp.	C	------	----------	----+-------	------+---	-
	E	------	----------	----------	----------	-
	Q				-------	-
Rhodomela confervoides	C	------	----------	----------++-	-+++++++++	-
	E	------	--------+++	+++++++++++	+++++--+++	+
	Q				--+++++	+
Derbesia marina	C	------	----+-------	----+-------	----------	-
	E	------	---------+--	----------	-------+++	+
	Q				----+++	+
Monostroma grevillei	C	------	----------	----------	----------	-
	E	------	----------	----+-------	----------	-
	Q				-------	-
Urospora wormskjoldii	C	------	----------	---+--------	---++-----	-
	E	------	----------	---+--------	---+------	-
	Q				-++----	-

Table 5. Species presence/absence from observations made monthly throughout the study at 6-9m.

SPECIES		1979 JASOND	1980 JFMAMJJASOND	1981 JFMAMJJASOND	1982 JFMAMJJASO..F
Acrothrix novaeangliae	C	++-----	----------	----------	------+++ -
	E	++-----	-----+++---	-----+++---	--------- -
	Q				---- -
Agarum cribrosum	C	------	----------	----------	--------- -
	E	------	----------	++++++++++	+++++++++ +
	Q				++++ -
Alaria esculenta	C	------	----------	----------	--------- -
	E	------	----------	--++++++++	+++++++++ +
	Q				++++ +
Chorda tomentosa	C	------	----------	----------	--------- -
	E	------	----------	--+++++++--	--------- -
	Q				---- -
Chordaria flagelliformis	C	+-----	----------	----------	-----+++ -
	E	------	-------+++++	++---+++++-	+++++++++ -
	Q				++++ +
Desmarestia aculeata	C	------	----------	----------	-----++++ +
	E	------	----------+	++++++++++	+++++++++ +
	Q				++++ +
Desmarestia viridis	C	------	----------	----------	--++++++ -
	E	------	----------+	++++++++--	+++++++++ -
	Q				++++ -
Dictyosiphon foeniculaceus	C	------	----------	----------	--------- -
	E	------	-------+++--	-----++++++	--------- -
	Q				-++- -
Ectocarpus spp.	C	+-----	----------	----------	-----++++ -
	E	+-----	-------+++++	++++++++++	+++++++++ -
	Q				++++ -
Eudesme virescens	C	++-----	----------	-----++-----	-----++++ -
	E	++-----	--------+++--	-----+++++-	-----+--- -
	Q				++++ -
Giffordia sp.	C	------	----------	----------	--------- -
	E	------	----------	-------+----	--------- -
	Q				---- -

Table 5, continued

Laminaria digitata	C	------	----------	----------	------+++	-
	E	------	---------++++	++++++++++	+++++++++	+
	Q				++++	+
Petalonia fascia	C	------	----------	----------	---------	-
	E	------	----------	----------	---------	-
	Q				-+++	-
Pilayella littoralis	C	------	----------	----------	------+++	-
	E	------	-------+++++	++++++++++-	---++++++	-
	Q				----	-
Saccorhiza dermatodea	C	------	----------	----------	---------	-
	E	------	----------	----++++++++	+--++++++	-
	Q				----	-
Scytosiphon lomentaria	C	------	----------	----------	---------	-
	E	------	----------	----++++++++	++--+++--	-
	Q				++++	-
Antithamnion pylaisaei	C	------	----------	----------	------+++	-
	E	------	-------++++	++++++++++	+++++++++	+
	Q				++++	+
Antithamnionella floccosa	C	------	----------	----------	---------	-
	E	------	----------+	++++++++++	++++++--++	+
	Q				----	+
Bonnemaisonia hamifera	C	------	--------+---	----------	---------	-
	E	------	----------	----------	---------	-
	Q				----	-
Callophyllis cristata	C	------	----------	----------	---------	-
	E	------	----------	-----+++++++	+++++++++	+
	Q				----	-
Ceramium rubrum	C	------	----------	----------	---------	-
	E	------	---------++++	+++++++++++	+++++++++	+
	Q				++++	+
Phycodrys rubens	C	------	----------	----------	---------	-
	E	------	----------	----------	-----+++	+
	Q				----	+
Polysiphonia flexicaulis	C	------	----------	----------	-----++++	-
	E	------	---------++++	++++++++++	+++++++++	+
	Q				++++	+
Polysiphonia urceolata	C	------	----------	----------	-----+++	-
	E	------	---------++++	++++++++++	+++++++++	+
	Q				++++	+

Table 5. continued

Ptilota serrata	C	------	----------	----------	---------	-
	E	------	----------	++++++++++	+++++++++	+
	Q				----	-
Rhodomela confervoides	C	------	----------	----------	---------	-
	E	------	--------++++	++++++++++	+++++++++	+
	Q				--++	+
Monostroma grevillei	C	------	----------	----------	---------	-
	E	------	----------	----+------	---------	-
	Q				----	-

Table 6. Comparison of species composition of the 2-3m and 6-9m areas on the experimental (E), quicklimed (Q), and control (C) transects during the macro-algal increase which occurred on the control transect during the summer of 1982. (Log mean is the mean of the log transformed biomass data originally in g m-2; Percentages calculated from arithmetic means).

(2-3m)	E (N=10)			Q (N=5)			C (N=10)		
Species	log mean	std. err.	% total	log mean	std. err.	% total	log mean	std. err.	% total
Alaria esculenta	2.86	0.33	98.5	2.27	0.74	94.3	0.27	0.16	0.62
Chorda tomentosa	0.23	0.23	0.84	0.0	--	0.0	0.24	0.24	4.18
Ceramium rubrum	0.38	0.19	0.24	+	--	+	+	--	+
Chordaria	0.24	0.18	0.23	0.19	0.19	0.07	1.25	0.22	6.90
Ectocarpus spp.*	0.17	0.13	0.09	0.78	0.49	2.46	1.85	0.23	24.7
Laminaria	0.16	0.13	0.07	0.49	0.37	0.73	0.0	--	0.0
P. urceolata	0.12	0.07	0.02	+	--	+	0.29	0.10	0.23
Desmarestia spp.	0.07	0.07	0.02	1.18	0.43	2.21	1.12	0.32	45.5
Rhodomela	0.06	0.04	0.01	+	--	+	+	--	+
Saccorhiza	0.05	0.05	0.01	0.0	--	0.0	0.22	0.15	0.42
Palmaria palmata	0.04	0.03	0.005	0.0	--	0.0	+	--	+
S. aeruginosa	+	--	+	0.0	--	0.0	0.06	0.06	0.04
S. pylaisaei	0.0	--	0.0	0.26	0.26	0.15	0.11	0.07	0.08
P. flexicaulis	0.0	--	0.0	0.30	0.14	0.06	+	--	+
Eudesme	0.0	--	0.0	0.18	0.14	0.04	1.71	0.23	15.1
P. zosterifolia	0.0	--	0.0	0.07	0.07	0.01	0.0	--	0.0
Dictyosiphon	0.0	--	0.0	0.0	--	0.0	0.58	0.20	1.39
Acrothrix	0.0	--	0.0	0.0	--	0.0	0.26	0.17	0.24
P. fascia	0.0	--	0.0	0.0	--	0.0	0.37	0.07	0.24
Ptilota serrata	0.0	--	0.0	0.0	--	0.0	+	--	+
Porphyra sp.	0.0	--	0.0	0.0	--	0.0	+	--	+
Pilayella	0.0	--	0.0	0.0	--	0.0	+	--	+
Devalaraea	0.0	--	0.0	0.0	--	0.0	+	--	+

Table 6, continued.

(6-9m)									
Desmarestia spp.	1.95	0.50	80.3	1.74	0.39	31.8	1.23	0.37	54.1
Laminaria	0.62	0.36	5.74	+	--	+	+	--	+
Alaria esculenta	0.58	0.37	5.46	0.58	0.54	14.5	0.0	--	0.0
P. flexicaulis	1.32	0.29	3.70	0.06	0.06	0.02	0.0	--	0.0
Agarum cribrosum	0.73	0.31	2.81	0.0	--	0.0	0.0	--	0.0
P. urceolata	0.44	0.22	0.50	0.23	0.17	0.21	0.18	0.11	0.25
Rhodomela	0.52	0.23	0.49	0.0	--	0.0	0.0	--	0.0
Chordaria	0.43	0.20	0.38	0.39	0.39	2.25	0.24	0.12	0.32
Ceramium rubrum	0.23	0.18	0.25	+	--	+	0.0	--	0.0
Ectocarpus spp.	0.32	0.15	0.16	1.68	0.61	49.4	1.70	0.30	30.1
Ptilota serrata	0.40	0.15	0.15	0.0	--	0.0	+	--	0.0
A. pylaisaei	0.14	0.12	0.08	0.03	0.02	0.01	0.04	0.03	0.02
Eudesme	0.08	0.05	0.01	0.44	0.34	1.62	1.44	0.28	14.3
Petalonia fascia	0.0	--	0.0	0.25	0.11	0.14	0.26	0.13	0.44
Dictyosiphon	0.0	--	0.0	+	--	+	0.18	0.12	0.29
Pilayella	0.0	--	0.0	+	--	+	0.0	--	0.0
Acrothrix	0.0	--	0.0	0.0	--	0.0	0.14	0.09	0.14

Table 7. The results of a survey of 18 sites in Conception Bay for percentage cover of macro-algae during the summer of 1982 (see text).

SITE	% COVER	BOTTOM TYPE
1	<10%	2
2	<10%	2
3	>50%	1
4	>50%	1
5	>50%	1
6	>50%	1
7	>50%	1
8	<10%	2
9	>50%	1
10	>50%	1
11	Algae on Tops of boulders only	2(largely)
12	>50%	1
13	>50%	1
14	<10%	2
15	<10%	1
16	Algae on Tops of boulders only	2(largely)
17	<10%	2
18	Algae on Tops of boulders only	2(largely)

Bottom types: 1=Coralline encrusted bedrock and large (>50 cm across) boulers, crevices abundant; 2=Coralline encrusted smooth bedrock, <5% boulders and/or crevices.

Table 8. Biomass (arithmetic mean) of algal species by year (the number in parentheses is the $\log_{10}$ mean ± std. err.; superscript on year indicates month during which ice scour occurred; + indicates presence but too little to weigh).

Species	1979^{Apr}	1980^{Feb}	1981	1982
	(N=10)	(N=14)	(N=13)	(N=20)
Chordaria flagelliformis	1329.4(2.95±.18)	92.1(1.22±.25)	1.99(.14±.11)	14.3(.25±.14)
Chordaria flagelliformis	1329.4(2.95±.18)	92.1(1.22±.25)	1.99(.14±.11)	14.3(.25±.14)
Alaria esculenta	718.3(2.15±.30)	1597.5(3.11±0.08)	5032.2(3.34±.31)	5780.0(3.28±0.24)
Saccorhiza dermatodea	7.6(.46±.19)	824.4(2.17±.31)	0.0	16.7(0.19±0.14)
Devaleraea ramentacea	119.4(1.35±.31)	177.3(1.31±.28)	6.7(.33±.16)	.61(.11±.05)
Spongomorpha arcta	31.1(1.16±0.23)	231.8(1.11±.30)	.55(.09±.07)	0.0
Spongomorpha aeruginosa	14.7(.95±.17)	2.39(.40±.09)	0.0	0.0
Dictyosiphon foeniculaceus	28.8(1.29±.15)	0.0	0.0	0.90(.06±.06)
Laminaria digitata	10.7(.30±.22)	3.18(.19±.12)	157.1(.46±.31)	14.3(.33±.15)
Scytosiphon lomentaria	18.8(.90±.18)	17.5(.56±.19)	0.0	.33(.07±.04)
Petalonia fascia	11.7(.87±.17)	22.2(0.66±.20)	+	99(.08±.07)
Petalonia zosterifolia	.11(.04±.02)	.11(.04±.02)	0.0	0.0
Phycodrys rubens	0.0	0.0	0.0	0.0
Pilayella littoralis	.75(.21±.05)	4.85(.33±.14)	.24(.07±.04)	+
Polysiphonia flexicaulis	.10(.03±.03)	.54(.09±.06)	.38(.08±.06)	+
Polysiphonia urceolata	11.7(.91±.15)	15.1(.71±.19)	51.6(.80±.25)	14.0(.54±.15)
Porphyra sp.	+	+	0.0	0.0
Ptilota serrata	+	0.0	0.0	+
Punctaria plantaginea	1.96(.30±.12)	.57(.07±.07)	0.0	0.0
Rhodomela confervoides	.23(.05±.05)	+	.88(.08±.08)	.53(.08±.06)
Scagelia corallina	+	+	+	+
Sphacelaria plumosa	0.0	0.0	0.0	0.0
Ulva lactuca	0.0	0.0	0.0	0.0
Ulvaria obscura	+	1.29(.16±.09)	.30(.07±.05)	0.0
Antithamnionella floccosa	+	0.0	0.0	0.0
Ceramium rubrum	.13(.04+.03)	+	5.59(.18±.14)	+
Chorda tomentosa	.58(.08±.08)	4.4(.21±.13)	0.0	0.0
Cystoclonium purpureum	0.0	+	0.0	0.0
Desmarestia spp.	0.0	0.0	17.9(.20±.18)	2.4(.08±.08)
Ectocarpus spp.	1.90(.28±.12)	28.3(.78±.23)	.12(.04±.03)	12.7(.34±.14)
Eudesme virescens	0.0	0.0	0.0	0.0
Giffordia granulosa	+	0.0	0.0	+
Monostroma grevillei	0.0	0.0	0.0	+
Palmaria palmata	+	.15(.04±.04)	.40(.07±.06)	4.13(.03±.01)

Table 9. Biomass data and summary statistics for urchins and molluscan herbivores.
A). Molluscan herbivores

TRST	DEPTH RANGE	SAMPLE PERIOD	N	ARITHMETIC MEAN BIOMASS	LOG_{10} BIOMASS	STD. ERR. LOG_{10} BIOMASS	% OF HERBIVORE BIOMASS
C	0-2M	SUM79	5	1.16	0.327	0.042	0.30
C	0-2M	SPR80	5	9.50	0.906	0.155	2.80
C	0-2M	AUT80	4	1.73	0.429	0.047	0.50
C	0-2M	SUM81	5	1.90	0.380	0.133	1.00
C	0-2M	SUM82	10	2.06	0.311	0.125	6.70
C	2-3M	SUM79	5	10.76	1.039	0.085	1.00
C	2-3M	AUT79	3	20.70	1.333	0.038	1.30
C	2-3M	SPR80	5	12.57	1.111	0.069	0.60
C	2-3M	SPR81	5	27.57	1.431	0.074	2.10
C	2-3M	SUM81	5	29.73	1.458	0.080	2.40
C	2-3M	SPR82	5	19.44	1.288	0.072	1.20
C	2-3M	SUM82	10	20.23	1.217	0.122	15.40
C	6-9M	SUM79	5	25.17	1.351	0.128	3.20
C	6-9M	AUT79	4	32.56	1.422	0.201	3.20
C	6-9M	SPR80	5	22.91	1.341	0.100	2.10
C	6-9M	AUT80	5	30.43	1.460	0.094	4.00
C	6-9M	SPR81	5	65.00	1.740	0.133	7.90
C	6-9M	SUM81	5	30.08	1.412	0.141	5.90
C	6-9M	SPR82	5	30.87	1.451	0.111	9.30
C	6-9M	SUM82	10	21.09	1.253	0.108	28.80
C	12-18M	SPR80	5	15.43	1.182	0.082	1.50
C	12-18M	SPR81	5	15.23	1.100	0.190	4.40
E	0-2M	SUM79	5	1.41	0.181	0.181	0.30
E	0-2M	AUT80	5	4.52	0.724	0.065	37.40
E	0-2M	SPR81	3	2.98	0.427	0.275	5.20
E	0-2M	SUM81	5	1.08	0.256	0.110	0.80
E	0-2M	SUM82	10	0.67	0.103	0.086	4.40
E	2-3M	SUM79	5	8.81	0.979	0.054	0.50
E	2-3M	AUT80	5	33.40	1.501	0.092	31.70
E	2-3M	SPR81	5	35.01	1.489	0.123	25.00
E	2-3M	SUM81	6	10.18	0.995	0.104	5.00
E	2-3M	SPR82	6	9.53	0.924	0.143	3.90
E	2-3M	SUM82	10	8.35	0.805	0.139	11.30
E	6-9M	SUM79	5	26.21	1.330	0.165	4.20
E	6-9M	AUT80	5	23.98	1.363	0.086	26.00
E	6-9M	SPR81	5	28.37	1.457	0.049	63.50
E	6-9M	SUM81	5	26.56	1.391	0.102	17.70
E	6-9M	SPR82	5	44.57	1.614	0.108	26.00
E	6-9M	SUM82	10	31.69	1.490	0.051	68.60
Q	2-3M	SPR82	5	23.44	1.378	0.049	20.90
Q	2-3M	SUM82	5	6.68	0.794	0.133	18.00
Q	6-9M	SUM82	5	7.18	0.695	0.213	16.00

Table 9 , cont'd

B). Urchins

TRST	DEPTH RANGE	SAMPLE PERIOD	N	ARITHMETIC MEAN BIOMASS	LOG_{10} BIOMASS	STD. ERR. LOG_{10} BIOMASS	% OF HERBIVORE BIOMASS
C	0-2M	SUM79	5	433.48	2.386	0.258	99.70
C	0-2M	SPR80	5	328.36	2.423	0.144	97.20
C	0-2M	AUT80	4	352.33	1.785	0.674	99.50
C	0-2M	SUM81	5	182.58	1.058	0.649	99.00
C	0-2M	SUM82	10	28.50	0.819	0.284	93.30
C	2-3M	SUM79	5	1074	2.988	0.092	99.00
C	2-3M	AUT79	3	1626	3.193	0.094	98.70
C	2-3M	SPR80	5	2019.5	3.262	0.101	99.40
C	2-3M	SPR81	5	1269.1	3.025	0.153	97.90
C	2-3M	SUM81	5	1207	3.071	0.050	97.60
C	2-3M	SPR82	5	1557.9	2.958	0.285	98.80
C	2-3M	SUM82	10	110.99	1.932	0.110	84.60
C	6-9M	SUM79	5	757.20	2.710	0.192	96.80
C	6-9M	AUT79	4	994.00	2.741	0.355	96.80
C	6-9M	SPR80	5	1079.5	2.989	0.102	97.90
C	6-9M	AUT80	5	736.14	2.385	0.450	96.00
C	6-9M	SPR81	5	755.28	2.836	0.100	92.10
C	6-9M	SUM81	5	484.00	2.493	0.239	94.10
C	6-9M	SPR82	5	299.60	2.227	0.240	90.70
C	6-9M	SUM82	10	52.21	1.208	0.257	71.20
C	12-18M	SPR80	5	1014.3	1.311	0.808	98.50
C	12-18M	SPR81	5	329.94	2.293	0.255	95.60
E	0-2M	SUM79	5	414.86	2.484	0.172	99.70
E	0-2M	AUT80	5	7.56	0.318	0.318	62.60
E	0-2M	SPR81	3	54.13	1.268	0.637	94.80
E	0-2M	SUM81	5	132.04	0.572	0.562	99.20
E	0-2M	SUM82	10	14.43	0.625	0.256	95.60
E	2-3M	SUM79	5	1800.2	3.230	0.072	99.50
E	2-3M	AUT80	5	71.90	1.665	0.210	68.30
E	2-3M	SPR81	5	104.98	1.714	0.289	75.00
E	2-3M	SUM81	6	194.58	2.220	0.116	95.00
E	2-3M	SPR82	6	232.90	1.527	0.508	96.10
E	2-3M	SUM82	10	65.71	1.429	0.266	88.70
E	6-9M	SUM79	5	597.60	2.771	0.036	95.80
E	6-9M	AUT80	5	68.26	1.566	0.280	74.00
E	6-9M	SPR81	5	16.30	1.023	0.217	36.50
E	6-9M	SUM81	5	123.18	1.752	0.305	82.30
E	6-9M	SPR82	5	126.72	1.665	0.337	74.00
E	6-9M	SUM82	10	14.52	0.932	0.178	31.40
Q	2-3M	SPR82	5	88.46	1.380	0.408	79.10
Q	2-3M	SUM82	5	30.34	1.347	0.218	82.00
Q	6-9M	SUM82	5	37.76	0.858	0.446	84.00

Table 10. Estimates of the percent of urchin biomass removed from the experimental transect for each depth (see text for explanation).

	CONTROL		EXPERIMENTAL		
Sample depth range	Geometric mean biomass	CV* (%)	Geometric mean biomass	CV* (%)	Estimated % removed
0-2m	65.1	64	5.3	143	-52<92<99.7
2-3m	1147.0	11	78.8	48	82<93<97
6-9m	323.0	29	37.9	44	66<88<96

*CV=(S/X) 100%

Table 11. Estimates of the percentage urchin biomass removed from the quicklimed transect, calculated by comparison with the untreated areas.

Geometric Mean Biomass ($g\ m^{-2}$)	C.V.* (%)	N	Estimated % Removal (with 95% confidence limits)	Sample Depth Range
69.8	46	10	$74 < 94 < 99$	2-3m
27.2	98	5	$-60 < 92 < 99.9$	6-9m

*C.V. = (S/X) x 100%

Table 12. Biomass and density data, and summary statistics for *Tonicella rubra*. (T=Transect: C=Control, E=Experimental, Q=Quicklimed; N=Number of samples).

T	DEPTH RANGE	SAMPLE PERIOD	N	ARITHMETIC MEAN BIOMASS	LOG_{10} BIOMASS	STD. ERR. LOG_{10} BIOMASS	ARITHMETIC MEAN DENSITY	LOG_{10} DENSITY	STD. ERR. LOG_{10} DENSITY	% OF HERBIVORE BIOMASS
C	0-2M	SUM79	5	0.26	0.072	0.072	4.00	0.264	0.264	0.10
C	0-2M	SPR80	5	0.43	0.126	0.077	4.00	0.417	0.255	0.10
C	0-2M	AUT80	4	0.41	0.105	0.105	2.50	0.260	0.260	0.10
C	0-2M	SUM81	5	0.38	0.116	0.071	4.00	0.417	0.255	0.20
C	0-2M	SUM82	10	0.36	0.089	0.059	5.00	0.369	0.189	1.20
C	2-3M	SUM79	5	10.20	1.017	0.087	114.00	2.020	0.098	0.90
C	2-3M	AUT79	3	15.63	1.215	0.049	216.67	2.322	0.082	0.90
C	2-3M	SPR80	5	12.05	1.091	0.072	138.00	2.114	0.081	0.60
C	2-3M	SPR81	5	25.95	1.402	0.080	256.00	2.389	0.067	2.00
C	2-3M	SUM81	5	27.78	1.431	0.077	324.00	2.443	0.119	2.20
C	2-3M	SPR82	5	15.44	1.202	0.055	234.00	2.344	0.074	1.00
C	2-3M	SUM82	10	17.25	1.128	0.130	182.00	2.136	0.140	13.10
C	6-9M	SUM79	5	20.48	1.282	0.110	374.00	2.516	0.125	2.60
C	6-9M	AUT79	4	26.54	1.347	0.189	552.50	2.709	0.107	2.60
C	6-9M	SPR80	5	10.95	0.941	0.219	248.00	2.256	0.207	1.00
C	6-9M	AUT80	5	20.62	1.292	0.093	806.00	2.860	0.098	2.70
C	6-9M	SPR81	5	39.70	1.514	0.152	916.00	2.906	0.121	4.80
C	6-9M	SUM81	5	25.54	1.347	0.138	746.00	2.833	0.098	5.00
C	6-9M	SPR82	5	29.50	1.430	0.112	880.00	2.893	0.110	8.90
C	6-9M	SUM82	10	17.65	1.167	0.111	543.00	2.560	0.141	24.10
C	12-18M	SPR80	5	6.61	0.877	0.031	254.00	2.396	0.047	0.60
C	12-18M	SPR81	5	8.99	0.860	0.178	176.00	2.225	0.074	2.60
E	0-2M	SUM79	5	0.00	0.000	0.000	0.00	0.000	0.000	0.00
E	0-2M	AUT80	5	0.00	0.000	0.000	0.00	0.000	0.000	0.00
E	0-2M	SPR81	3	2.33	0.311	0.294	16.67	0.885	0.472	4.10
E	0-2M	SUM81	5	0.00	0.000	0.000	0.00	0.000	0.000	0.00
E	0-2M	SUM82	10	0.22	0.051	0.051	3.00	0.312	0.159	1.50
E	2-3M	SUM79	5	5.66	0.751	0.134	52.00	1.636	0.159	0.30
E	2-3M	AUT80	5	6.52	0.670	0.228	70.00	1.384	0.409	6.20
E	2-3M	SPR81	5	6.73	0.866	0.071	44.00	1.631	0.068	4.80
E	2-3M	SUM81	6	7.62	0.855	0.130	76.67	1.853	0.082	3.70
E	2-3M	SPR82	6	5.90	0.675	0.186	40.00	1.276	0.305	2.40
E	2-3M	SUM82	10	6.39	0.643	0.158	49.00	1.468	0.197	8.60
E	6-9M	SUM79	5	19.69	1.253	0.134	710.00	2.747	0.187	3.20
E	6-9M	AUT80	5	20.38	1.299	0.079	628.00	2.738	0.105	22.10
E	6-9M	SPR81	5	18.73	1.293	0.021	610.00	2.772	0.056	41.90
E	6-9M	SUM81	5	16.94	1.086	0.205	712.00	2.631	0.252	11.30
E	6-9M	SPR82	5	27.10	1.380	0.121	980.00	2.889	0.169	15.80
E	6-9M	SUM82	10	24.96	1.366	0.072	927.00	2.901	0.089	54.00
Q	2-3M	SPR82	5	8.54	0.960	0.067	98.00	1.913	0.140	7.60
Q	2-3M	SUM82	5	4.34	0.503	0.229	52.00	1.110	0.467	11.70
Q	6-9M	SUM82	5	6.06	0.638	0.201	182.00	1.901	0.279	13.50

Table 13. Biomass and density data, and summary statistics for *Tonicella marmorea*. (T=Transect: C=Control, E=Experimental, Q=Quicklimed; N=Number of samples).

T	DEPTH RANGE	SAMPLE PERIOD	N	ARITHMETIC MEAN BIOMASS	LOG_{10} BIOMASS	STD. ERR. LOG_{10} BIOMASS	ARITHMETIC MEAN DENSITY	LOG_{10} DENSITY	STD. ERR. LOG_{10} DENSITY	% OF HERBIVORE BIOMASS
C	0-2M	SUM79	5	0.00	0.000	0.000	0.00	0.000	0.000	0.00
C	0-2M	SPR80	5	0.00	0.000	0.000	0.00	0.000	0.000	0.00
C	0-2M	AUT80	4	0.00	0.000	0.000	0.00	0.000	0.000	0.00
C	0-2M	SUM81	5	0.00	0.000	0.000	0.00	0.000	0.000	0.00
C	0-2M	SUM82	10	0.00	0.000	0.000	0.00	0.000	0.000	0.00
C	2-3M	SUM79	5	0.00	0.000	0.000	0.00	0.000	0.000	0.00
C	2-3M	AUT79	3	0.00	0.000	0.000	0.00	0.000	0.000	0.00
C	2-3M	SPR80	5	0.00	0.000	0.000	0.00	0.000	0.000	0.00
C	2-3M	SPR81	5	0.00	0.000	0.000	0.00	0.000	0.000	0.00
C	2-3M	SUM81	5	0.35	0.095	0.081	2.20	0.268	0.202	0.00
C	2-3M	SPR82	5	0.00	0.000	0.000	0.00	0.000	0.000	0.00
C	2-3M	SUM82	10	0.00	0.000	0.000	0.00	0.000	0.000	0.00
C	6-9M	SUM79	5	2.88	0.414	0.193	36.00	0.986	0.424	0.40
C	6-9M	AUT79	4	3.08	0.436	0.213	57.50	1.458	0.287	0.30
C	6-9M	SPR80	5	6.92	0.765	0.204	58.00	1.460	0.374	0.60
C	6-9M	AUT80	5	8.92	0.627	0.285	60.00	1.316	0.394	1.20
C	6-9M	SPR81	5	20.46	1.261	0.125	108.00	1.934	0.149	2.50
C	6-9M	SUM81	5	2.02	0.340	0.168	18.00	0.870	0.362	0.40
C	6-9M	SPR82	5	0.02	0.008	0.008	4.00	0.264	0.264	0.00
C	6-9M	SUM82	10	2.01	0.285	0.127	20.00	0.629	0.268	2.70
C	12-18M	SPR80	5	8.74	0.914	0.124	60.00	1.664	0.182	0.80
C	12-18M	SPR81	5	5.44	0.637	0.212	42.00	1.336	0.350	1.60
E	0-2M	SUM79	5	0.00	0.000	0.000	0.00	0.000	0.000	0.00
E	0-2M	AUT80	5	0.00	0.000	0.000	0.00	0.000	0.000	0.00
E	0-2M	SPR81	3	0.00	0.000	0.000	0.00	0.000	0.000	0.00
E	0-2M	SUM81	5	0.00	0.000	0.000	0.00	0.000	0.000	0.00
E	0-2M	SUM82	10	0.00	0.000	0.000	20.00	0.401	0.267	0.00
E	2-3M	SUM79	5	0.00	0.000	0.000	0.00	0.000	0.000	0.00
E	2-3M	AUT80	5	0.00	0.000	0.000	0.00	0.000	0.000	0.00
E	2-3M	SPR81	5	0.00	0.000	0.000	0.00	0.000	0.000	0.00
E	2-3M	SUM81	6	0.00	0.000	0.000	0.00	0.000	0.000	0.00
E	2-3M	SPR82	6	0.00	0.000	0.000	0.00	0.000	0.000	0.00
E	2-3M	SUM82	10	0.08	0.026	0.026	1.00	0.104	0.104	0.10
E	6-9M	SUM79	5	5.82	0.456	0.264	140.00	1.250	0.549	0.90
E	6-9M	AUT80	5	1.48	0.291	0.145	20.00	0.843	0.368	1.60
E	6-9M	SPR81	5	2.44	0.384	0.181	26.00	0.874	0.390	5.50
E	6-9M	SUM81	5	3.02	0.449	0.178	26.00	1.097	0.318	2.00
E	6-9M	SPR82	5	8.36	0.545	0.288	80.00	1.123	0.496	4.90
E	6-9M	SUM82	10	2.56	0.476	0.092	71.00	1.515	0.221	5.50
Q	2-3M	SPR82	5	1.42	0.182	0.182	4.00	0.264	0.264	1.30
Q	2-3M	SUM82	5	0.00	0.000	0.000	0.00	0.000	0.000	0.00
Q	6-9M	SUM82	5	0.10	0.035	0.035	2.00	0.208	0.208	0.20

Table 14. Biomass and density data, and summary statistics for *Ischnochiton alba*. (T=Transect: C=Control, E=Experimental,Q=Quicklimed; N=Number of samples).

T	DEPTH RANGE	SAMPLE PERIOD	N	ARITHMETIC MEAN BIOMASS	LOG_{10} BIOMASS	STD. ERR. LOG_{10} BIOMASS	ARITHMETIC MEAN DENSITY	LOG_{10} DENSITY	STD. ERR. LOG_{10} DENSITY	% OF HERBIVORE BIOMASS
C	0-2M	SUM79	5	0.00	0.000	0.000	0.00	0.000	0.000	0.00
C	0-2M	SPR80	5	0.00	0.000	0.000	0.00	0.000	0.000	0.00
C	0-2M	AUT80	4	0.00	0.000	0.000	0.00	0.000	0.000	0.00
C	0-2M	SUM81	5	0.00	0.000	0.000	0.00	0.000	0.000	0.00
C	0-2M	SUM82	10	0.00	0.000	0.000	0.00	0.000	0.000	0.00
C	2-3M	SUM79	5	0.00	0.000	0.000	0.00	0.000	0.000	0.00
C	2-3M	AUT79	3	0.00	0.000	0.000	0.00	0.000	0.000	0.00
C	2-3M	SPR80	5	0.00	0.000	0.000	0.00	0.000	0.000	0.00
C	2-3M	SPR81	5	0.00	0.000	0.000	0.00	0.000	0.000	0.00
C	2-3M	SUM81	5	0.00	0.000	0.000	0.00	0.000	0.000	0.00
C	2-3M	SPR82	5	0.00	0.000	0.000	0.00	0.000	0.000	0.00
C	2-3M	SUM82	10	0.00	0.000	0.000	0.00	0.000	0.000	0.00
C	6-9M	SUM79	5	0.00	0.000	0.000	0.00	0.000	0.000	0.00
C	6-9M	AUT79	4	0.49	0.117	0.117	5.00	0.331	0.331	0.00
C	6-9M	SPR80	5	0.11	0.042	0.024	10.00	0.737	0.305	0.00
C	6-9M	AUT80	5	0.00	0.000	0.000	0.00	0.000	0.000	0.00
C	6-9M	SPR81	5	0.10	0.036	0.036	6.00	0.298	0.298	0.00
C	6-9M	SUM81	5	0.00	0.000	0.000	0.00	0.000	0.000	0.00
C	6-9M	SPR82	5	0.30	0.080	0.080	14.00	0.621	0.381	0.10
C	6-9M	SUM82	10	0.11	0.032	0.032	3.00	0.149	0.149	0.20
C	12-18M	SPR80	5	0.00	0.000	0.000	0.00	0.000	0.000	0.00
C	12-18M	SPR81	5	0.00	0.000	0.000	0.00	0.000	0.000	0.00
E	0-2M	SUM79	5	0.00	0.000	0.000	0.00	0.000	0.000	0.00
E	0-2M	AUT80	5	0.00	0.000	0.000	0.00	0.000	0.000	0.00
E	0-2M	SPR81	3	0.00	0.000	0.000	0.00	0.000	0.000	0.00
E	0-2M	SUM81	5	0.00	0.000	0.000	0.00	0.000	0.000	0.00
E	0-2M	SUM82	10	0.00	0.000	0.000	0.00	0.000	0.000	0.00
E	2-3M	SUM79	5	0.00	0.000	0.000	0.00	0.000	0.000	0.00
E	2-3M	AUT80	5	0.00	0.000	0.000	0.00	0.000	0.000	0.00
E	2-3M	SPR81	5	0.00	0.000	0.000	0.00	0.000	0.000	0.00
E	2-3M	SUM81	6	0.00	0.000	0.000	0.00	0.000	0.000	0.00
E	2-3M	SPR82	6	0.00	0.000	0.000	0.00	0.000	0.000	0.00
E	2-3M	SUM82	10	0.00	0.000	0.000	0.00	0.000	0.000	0.00
E	6-9M	SUM79	5	0.00	0.000	0.000	0.00	0.000	0.000	0.00
E	6-9M	AUT80	5	0.00	0.000	0.000	0.00	0.000	0.000	0.00
E	6-9M	SPR81	5	0.02	0.008	0.008	2.00	0.208	0.208	0.00
E	6-9M	SUM81	5	0.18	0.062	0.045	8.00	0.507	0.318	0.10
E	6-9M	SPR82	4	0.75	0.151	0.151	5.00	0.331	0.331	0.40
E	6-9M	SUM82	10	0.14	0.049	0.023	7.00	0.501	0.206	0.30
Q	2-3M	SPR82	5	0.00	0.000	0.000	0.00	0.000	0.000	0.00
Q	2-3M	SUM82	5	0.00	0.000	0.000	0.00	0.000	0.000	0.00
Q	6-9M	SUM82	5	0.00	0.000	0.000	0.00	0.000	0.000	0.00

Table 15. Biomass and density data, and summary statistics for *Acmaea testudinalis* (T=Transect: C=Control, E=Experimental, Q=Quicklimed; N=Number of samples).

T	DEPTH RANGE	SAMPLE PERIOD	N	ARITHMETIC MEAN BIOMASS	LOG_{10} BIOMASS	STD. ERR. LOG_{10} BIOMASS	ARITHMETIC MEAN DENSITY	LOG_{10} DENSITY	STD. ERR. LOG_{10} DENSITY	% OF HERBIVORE BIOMASS
C	0-2M	SUM79	5	0.80	0.235	0.069	10.00	0.889	0.229	0.20
C	0-2M	SPR80	5	3.00	0.360	0.226	10.00	0.531	0.337	0.90
C	0-2M	AUT80	4	0.30	0.091	0.078	10.00	0.851	0.291	0.10
C	0-2M	SUM81	3	2.47	0.435	0.231	16.67	0.938	0.471	1.30
C	0-2M	SUM82	10	1.70	0.265	0.117	17.00	0.735	0.253	5.60
C	2-3M	SUM79	5	0.56	0.157	0.087	10.00	0.715	0.303	0.10
C	2-3M	AUT79	3	1.37	0.323	0.155	36.67	1.424	0.255	0.10
C	2-3M	SPR80	5	0.17	0.058	0.041	10.00	0.715	0.303	0.00
C	2-3M	SPR81	5	1.62	0.346	0.127	46.00	1.539	0.155	0.10
C	2-3M	SUM81	5	1.58	0.370	0.102	54.00	1.443	0.368	0.10
C	2-3M	SPR82	5	2.58	0.467	0.143	86.00	1.779	0.199	0.20
C	2-3M	SUM82	10	2.68	0.470	0.101	66.00	1.571	0.209	2.00
C	6-9M	SUM79	5	1.79	0.404	0.102	48.00	1.529	0.205	0.20
C	6-9M	AUT79	4	2.20	0.463	0.122	130.00	1.981	0.232	0.20
C	6-9M	SPR80	5	4.92	0.731	0.098	122.00	2.004	0.150	0.40
C	6-9M	AUT80	5	0.67	0.181	0.094	52.00	1.088	0.466	0.10
C	6-9M	SPR81	5	4.69	0.675	0.141	104.00	1.939	0.141	0.60
C	6-9M	SUM81	5	2.52	0.419	0.165	72.00	1.512	0.393	0.50
C	6-9M	SPR82	5	1.03	0.255	0.107	46.00	1.383	0.356	0.30
C	6-9M	SUM82	10	1.12	0.278	0.068	41.00	1.429	0.182	1.50
C	12-18M	SPR80	5	0.08	0.028	0.028	4.00	0.264	0.264	0.00
C	12-18M	SPR81	5	0.13	0.049	0.030	6.00	0.298	0.298	0.00
E	0-2M	SUM79	5	1.41	0.181	0.181	4.00	0.264	0.264	0.30
E	0-2M	AUT80	5	0.00	0.000	0.000	2.00	0.208	0.208	0.00
E	0-2M	SPR81	3	0.44	0.146	0.074	16.67	0.938	0.471	0.80
E	0-2M	SUM81	5	0.18	0.068	0.030	8.00	0.681	0.283	0.10
E	0-2M	SUM82	10	0.45	0.088	0.070	3.00	0.236	0.159	3.00
E	2-3M	SUM79	5	3.15	0.527	0.151	32.00	1.440	0.132	0.20
E	2-3M	AUT80	5	3.82	0.426	0.218	14.00	0.979	0.259	3.60
E	2-3M	SPR81	5	6.88	0.570	0.231	86.00	1.914	0.080	4.90
E	2-3M	SUM81	6	2.13	0.463	0.075	96.67	1.962	0.075	1.00
E	2-3M	SPR82	6	0.79	0.227	0.066	36.67	1.504	0.118	0.30
E	2-3M	SUM82	10	1.59	0.345	0.084	54.00	1.280	0.287	2.10
E	6-9M	SUM79	5	0.70	0.200	0.081	64.00	1.711	0.151	0.10
E	6-9M	AUT80	5	0.49	0.123	0.096	26.00	0.898	0.394	0.50
E	6-9M	SPR81	5	6.19	0.663	0.220	128.00	1.747	0.441	13.80
E	6-9M	SUM81	5	6.38	0.698	0.171	148.00	2.079	0.139	4.30
E	6-9M	SPR82	5	1.86	0.401	0.117	78.00	1.850	0.109	1.10
E	6-9M	SUM82	10	2.14	0.435	0.078	76.00	1.685	0.200	4.60
Q	2-3M	SPR82	5	2.94	0.573	0.072	76.00	1.883	0.030	2.60
Q	2-3M	SUM82	5	1.12	0.274	0.103	24.00	1.215	0.173	3.00
Q	6-9M	SUM82	5	0.90	0.204	0.126	18.00	0.655	0.404	2.00

Table 16. Biomass and density data, and summary statistics for *Lacuna vincta*. (T=Transect: C=Control, E=Experimental, Q=Quicklimed; N=Number of samples).

T	DEPTH RANGE	SAMPLE PERIOD	N	ARITHMETIC MEAN BIOMASS	LOG_{10} BIOMASS	STD. ERR. LOG_{10} BIOMASS	ARITHMETIC MEAN DENSITY	LOG_{10} DENSITY	STD. ERR. LOG_{10} DENSITY	% OF HERBIVORE BIOMASS
C	0-2M	SUM79	5	0.02	0.008	0.008	2.00	0.208	0.208	0.00
C	0-2M	SPR80	5	1.21	0.302	0.098	64.00	1.495	0.383	0.40
C	0-2M	AUT80	4	0.98	0.290	0.041	807.50	2.874	0.100	0.30
C	0-2M	SUM81	5	0.00	0.000	0.000	0.00	0.000	0.000	0.00
C	0-2M	SUM82	10	0.00	0.000	0.000	0.00	0.000	0.000	0.00
C	2-3M	SUM79	5	0.00	0.001	0.001	2.00	0.208	0.208	0.00
C	2-3M	AUT79	3	0.21	0.080	0.024	193.33	2.104	0.280	0.00
C	2-3M	SPR80	5	0.00	0.000	0.000	0.00	0.000	0.000	0.00
C	2-3M	AUT80*	5	0.55	0.183	0.040	613.80	2.534	0.250	-
C	2-3M	SPR81	5	0.00	0.000	0.000	0.00	0.000	0.000	0.00
C	2-3M	SUM81	5	0.00	0.000	0.000	2.00	0.208	0.208	0.00
C	2-3M	SPR82	5	1.38	0.206	0.169	44.00	1.001	0.448	0.10
C	2-3M	SUM82	10	0.30	0.060	0.060	3.00	0.236	0.159	0.20
C	6-9M	SUM79	5	0.00	0.000	0.000	0.00	0.000	0.000	0.00
C	6-9M	AUT79	4	0.16	0.064	0.016	165.00	2.077	0.253	0.00
C	6-9M	SPR80	5	0.00	0.000	0.000	0.00	0.000	0.000	0.00
C	6-9M	AUT80	5	0.22	0.076	0.046	46.00	1.624	0.101	0.00
C	6-9M	SPR81	5	0.00	0.000	0.000	4.00	0.264	0.264	0.00
C	6-9M	SUM81	5	0.00	0.000	0.000	10.00	0.563	0.346	0.00
C	6-9M	SPR82	5	0.02	0.008	0.008	12.00	0.357	0.357	0.00
C	6-9M	SUM82	10	0.20	0.050	0.046	42.00	0.572	0.273	0.30
C	12-18M	SPR80	5	0.00	0.000	0.000	0.00	0.000	0.000	0.00
C	12-18M	SPR81	5	0.67	0.209	0.054	108.00	1.971	0.120	0.20
E	0-2M	SUM79	5	0.00	0.000	0.000	0.00	0.000	0.000	0.00
E	0-2M	AUT80	5	4.32	0.708	0.063	2272.00	3.073	0.280	35.80
E	0-2M	SPR81	3	0.03	0.012	0.012	6.67	0.441	0.441	0.10
E	0-2M	SUM81	5	0.64	0.168	0.095	146.00	1.519	0.449	0.50
E	0-2M	SUM82	10	0.00	0.000	0.000	0.00	0.000	0.000	0.00
E	2-3M	SUM79	5	0.00	0.000	0.000	0.00	0.000	0.000	0.00
E	2-3M	AUT80	5	21.54	1.327	0.077	4815.00	3.629	0.117	20.50
E	2-3M	SPR81	5	14.30	1.043	0.164	2058.00	3.017	0.253	10.20
E	2-3M	SUM81	6	0.22	0.078	0.035	68.33	1.316	0.422	0.10
E	2-3M	SPR82	6	1.23	0.299	0.093	295.00	2.252	0.221	0.50
E	2-3M	SUM82	10	0.29	0.092	0.040	80.00	1.415	0.271	0.40
E	6-9M	SUM79	5	0.00	0.000	0.000	6.00	0.473	0.293	0.00
E	6-9M	AUT80	5	1.55	0.235	0.170	1485.00	2.629	0.399	1.70
E	6-9M	SPR81	5	0.89	0.254	0.071	438.00	2.514	0.184	2.00
E	6-9M	SUM81	5	0.00	0.000	0.000	12.00	0.587	0.382	0.00
E	6-9M	SPR82	5	4.71	0.624	0.185	573.00	2.347	0.379	2.70
E	6-9M	SUM82	10	1.89	0.296	0.114	852.00	2.032	0.410	4.10
Q	2-3M	SPR82	5	8.14	0.934	0.081	2536.00	3.177	0.207	7.30
Q	2-3M	SUM82	5	1.10	0.262	0.116	1048.00	2.045	0.661	3.00
Q	6-9M	SUM82	5	0.10	0.039	0.024	42.00	0.721	0.467	0.20

*data from quadrats taken outside the experimental transect. Only *Lacuna* and *Margarites* quantified.

Table 17. Calculation of the survival into the following spring and summer of *Lacuna* from the autumn 1980 recruitment (nd=no data, T=Transect: C=Control, E=Experimental).

		0-2m		2-3m		6-9m	
Date	T	Geometric mean density		Geometric mean density		Geometric mean density	
Aut80	C	nd	%	340.9	%	41.1	%
	E	1181.0	surviving	4250.6	surviving	424.2	surviving
Spr81	C	nd	nd	0.0	0.0	0.84	2.04
	E	1.76	0.02	1038.8	24.4	325.7	76.8
Sum81	C	nd	nd	0.6	0.02	2.65	6.45
	E	32.0	2.7	19.7	0.46	2.86	0.67

Table 18. Biomass and density data, and summary statistics for *Margarites helicinus*. (T=Transect: C=Control, E=Experimental, Q=Quicklimed; N=Number of samples).

T	DEPTH RANGE	SAMPLE PERIOD	N	ARITHMETIC MEAN BIOMASS	LOG_{10} BIOMASS	STD. ERR. LOG_{10} BIOMASS	ARITHMETIC MEAN DENSITY	LOG_{10} DENSITY	STD. ERR. LOG_{10} DENSITY	% OF HERBIVORE BIOMASS
C	0-2M	SUM79	5	0.08	0.031	0.022	6.00	0.473	0.293	0.00
C	0-2M	SPR80	5	4.86	0.670	0.144	454.00	2.494	0.195	1.40
C	0-2M	AUT80*	4	0.05	0.021	0.012	102.50	1.832	0.248	-
C	0-2M	SUM81	5	0.04	0.016	0.016	48.00	1.352	0.361	0.00
C	0-2M	SUM82	10	0.00	0.000	0.000	0.00	0.000	0.000	0.00
C	2-3M	SUM79	5	0.00	0.000	0.000	2.00	0.208	0.208	0.00
C	2-3M	AUT79	3	3.49	0.640	0.074	1556.67	3.182	0.068	0.20
C	2-3M	SPR80	5	0.36	0.100	0.079	42.00	0.953	0.433	0.00
C	2-3M	SPR81	5	0.00	0.000	0.000	0.00	0.000	0.000	0.00
C	2-3M	SUM81	5	0.02	0.008	0.008	38.00	1.037	0.435	0.00
C	2-3M	SPR82	5	0.04	0.016	0.016	2.00	0.208	0.208	0.00
C	2-3M	SUM82	10	0.00	0.000	0.000	2.00	0.208	0.139	0.00
C	6-9M	SUM79	5	0.02	0.007	0.007	2.00	0.208	0.208	0.00
C	6-9M	AUT79	4	0.10	0.038	0.023	65.00	1.056	0.610	0.00
C	6-9M	SPR80	5	0.02	0.009	0.006	4.00	0.417	0.255	0.00
C	6-9M	AUT80	5	0.00	0.000	0.000	10.00	0.737	0.305	0.00
C	6-9M	SPR81	5	0.04	0.016	0.016	2.00	0.208	0.208	0.00
C	6-9M	SUM81	5	0.00	0.000	0.000	0.00	0.000	0.000	0.00
C	6-9M	SPR82	5	0.00	0.001	0.001	2.00	0.208	0.208	0.00
C	6-9M	SUM82	10	0.00	0.000	0.000	0.00	0.000	0.000	0.00
C	12-18M	SPR80	5	0.00	0.000	0.000	0.00	0.000	0.000	0.00
C	12-18M	SPR81	5	0.00	0.000	0.000	0.00	0.000	0.000	0.00
E	0-2M	SUM79	5	0.00	0.000	0.000	0.00	0.000	0.000	0.00
E	0-2M	AUT80	5	0.20	0.067	0.050	168.00	1.220	0.556	1.70
E	0-2M	SPR81	3	0.17	0.061	0.061	26.67	0.636	0.636	0.30
E	0-2M	SUM81	5	0.26	0.083	0.059	144.00	1.474	0.478	0.20
E	0-2M	SUM82	10	0.00	0.000	0.000	0.00	0.000	0.000	0.00
E	2-3M	SUM79	5	0.00	0.000	0.000	0.00	0.000	0.000	0.00
E	2-3M	AUT80	5	1.51	0.371	0.084	1530.00	3.091	0.149	1.40
E	2-3M	SPR81	5	7.10	0.810	0.151	640.00	2.741	0.125	5.10
E	2-3M	SUM81	6	0.22	0.078	0.035	61.67	1.022	0.462	0.10
E	2-3M	SPR82	6	1.62	0.252	0.155	128.33	1.107	0.516	0.70
E	2-3M	SUM82	10	0.00	0.000	0.000	2.00	0.132	0.132	0.00
E	6-9M	SUM79	5	0.00	0.000	0.000	0.00	0.000	0.000	0.00
E	6-9M	AUT80	5	0.08	0.032	0.015	55.00	1.132	0.473	0.10
E	6-9M	SPR81	5	0.11	0.041	0.025	24.00	0.888	0.388	0.20
E	6-9M	SUM81	5	0.04	0.016	0.016	6.00	0.298	0.298	0.00
E	6-9M	SPR82	5	1.94	0.240	0.193	130.00	1.194	0.537	1.10
E	6-9M	SUM82	10	0.00	0.000	0.000	10.00	0.200	0.200	0.00
Q	2-3M	SPR82	5	2.40	0.476	0.115	96.00	1.834	0.215	2.10
Q	2-3M	SUM82	5	0.12	0.046	0.027	122.00	1.356	0.560	0.30
Q	6-9M	SUM82	5	0.02	0.008	0.008	28.00	0.430	0.430	0.00

*data from quadrats taken outside the experimental transect.$Only *Lacuna* and *Margarites* quantified.

Table 19. Calculation of the survival into the following spring and summer of *Margarites* from the autumn 1979 recruitment (T = transect: E = experimental, C = control; nd=no data).

		0-2m		2-3m		6-9m	
Date	T	Geometric mean density		Geometric mean density		Geometric mean density	
Aut80	C	nd	%	789.7	%	4.5	%
	E	15.6	surviving	1231.8	surviving	12.6	surviving
Spr81	C	nd	nd	0.0	0.0	0.6	13.3
	E	3.3	21.2	549.7	44.7	6.7	53.2
Sum81	C	nd	nd	9.9	1.25	0.0	0.0
	E	28.8	184.5	9.5	0.77	1.9	15.1

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Appendix A. Biomass data for each species of macro-alga sampled during the present study (T=Transect: E=Experimental, C=Control, Q=Quicklimed; N=Number of quadrats)

Species=*ACROTHRIX NOVAEANGLIAE*

Depth range	Sample period	T	N	Arithmetic Mean	Mean of log transformed data	Standard error (log_{10})	Geometric Mean	Percent of biomass
0-2m	SUM79	E	5	0.000	0.000	0.00	0.000	0.00
0-2m	SPR80	C	5	0.000	0.000	0.00	0.000	0.00
0-2m	AUT80	C	4	0.000	0.000	0.00	0.000	0.00
0-2m	AUT80	E	5	0.000	0.000	0.00	0.000	0.00
0-2m	SPR81	E	3	0.000	0.000	0.00	0.000	0.00
0-2m	SUM81	C	5	0.000	0.000	0.00	0.000	0.00
0-2m	SUM81	E	5	0.000	0.000	0.00	0.000	0.00
0-2m	SUM82	C	10	0.000	0.000	0.00	0.000	0.00
0-2m	SUM82	E	10	0.000	0.000	0.00	0.000	0.00
2-3m	SUM79	C	5	0.000	0.000	0.00	0.000	0.00
2-3m	SUM79	E	5	0.000	0.000	0.00	0.000	0.00
2-3m	AUT79	C	3	0.000	0.000	0.00	0.000	0.00
2-3m	SPR80	C	5	0.000	0.000	0.00	0.000	0.00
2-3m	AUT80	E	5	0.000	0.000	0.00	0.000	0.00
2-3m	SPR81	C	5	0.000	0.000	0.00	0.000	0.00
2-3m	SPR81	E	5	0.000	0.000	0.00	0.000	0.00
2-3m	SUM81	C	5	0.000	0.000	0.00	0.000	0.00
2-3m	SUM81	E	6	0.000	0.000	0.00	0.000	0.00
2-3m	SPR82	C	5	0.000	0.000	0.00	0.000	0.00
2-3m	SPR82	E	6	0.000	0.000	0.00	0.000	0.00
2-3m	SPR82	Q	5	0.000	0.000	0.00	0.000	0.00
2-3m	SUM82	C	10	3.400	0.260	0.17	0.800	0.50
2-3m	SUM82	E	10	0.000	0.000	0.00	0.000	0.00
2-3m	SUM82	Q	5	0.000	0.000	0.00	0.000	0.00
6-9m	SUM79	C	5	0.000	0.000	0.00	0.000	0.00
6-9m	SUM79	E	5	0.000	0.000	0.00	0.000	0.00
6-9m	AUT79	C	4	0.000	0.000	0.00	0.000	0.00
6-9m	SPR80	C	5	0.000	0.000	0.00	0.000	0.00
6-9m	AUT80	C	5	0.000	0.000	0.00	0.000	0.00
6-9m	AUT80	E	5	0.000	0.000	0.00	0.000	0.00
6-9m	SPR81	C	5	0.000	0.000	0.00	0.000	0.00
6-9m	SPR81	E	5	0.000	0.000	0.00	0.000	0.00
6-9m	SUM81	C	5	0.000	0.000	0.00	0.000	0.00
6-9m	SUM81	E	5	0.000	0.000	0.00	0.000	0.00
6-9m	SPR82	C	5	0.000	0.000	0.00	0.000	0.00
6-9m	SPR82	E	5	0.000	0.000	0.00	0.000	0.00
6-9m	SUM82	C	10	0.800	0.140	0.09	0.400	0.10
6-9m	SUM82	E	10	0.000	0.000	0.00	0.000	0.00
6-9m	SUM82	Q	5	0.000	0.000	0.00	0.000	0.00

Appendix A, Continued

Species=*AGARUM CRIBROSUM*

Depth range	Sample period	T	N	Arithmetic Mean	Mean of log transformed data	Standard error (log_{10})	Geometric Mean	Percent of biomass
0-2m	SUM79	C	5	0.000	0.000	0.00	0.000	0.00
0-2m	SUM79	E	5	0.000	0.000	0.00	0.000	0.00
0-2m	SPR80	C	5	0.000	0.000	0.00	0.000	0.00
0-2m	AUT80	C	4	0.000	0.000	0.00	0.000	0.00
0-2m	AUT80	E	5	0.000	0.000	0.00	0.000	0.00
0-2m	SPR81	E	3	0.000	0.000	0.00	0.000	0.00
0-2m	SUM81	C	5	0.000	0.000	0.00	0.000	0.00
0-2m	SUM81	E	5	0.000	0.000	0.00	0.000	0.00
0-2m	SUM82	C	10	0.000	0.000	0.00	0.000	0.00
0-2m	SUM82	E	10	0.000	0.000	0.00	0.000	0.00
2-3m	SUM79	C	5	0.000	0.000	0.00	0.000	0.00
2-3m	SUM79	E	5	0.000	0.000	0.00	0.000	0.00
2-3m	AUT79	C	3	0.000	0.000	0.00	0.000	0.00
2-3m	SPR80	C	5	0.000	0.000	0.00	0.000	0.00
2-3m	AUT80	E	5	0.000	0.000	0.00	0.000	0.00
2-3m	SPR81	C	5	0.000	0.000	0.00	0.000	0.00
2-3m	SPR81	E	5	0.000	0.000	0.00	0.000	0.00
2-3m	SUM81	C	5	0.000	0.000	0.00	0.000	0.00
2-3m	SUM81	E	6	0.000	0.000	0.00	0.000	0.00
2-3m	SPR82	C	5	0.000	0.000	0.00	0.000	0.00
2-3m	SPR82	E	6	0.000	0.000	0.00	0.000	0.00
2-3m	SPR82	Q	5	0.000	0.000	0.00	0.000	0.00
2-3m	SUM82	C	10	0.000	0.000	0.00	0.000	0.00
2-3m	SUM82	E	10	0.000	0.000	0.00	0.000	0.00
2-3m	SUM82	Q	5	0.000	0.000	0.00	0.000	0.00
6-9m	SUM79	C	5	0.000	0.000	0.00	0.000	0.00
6-9m	SUM79	E	5	0.000	0.000	0.00	0.000	0.00
6-9m	AUT79	C	4	0.000	0.000	0.00	0.000	0.00
6-9m	SPR80	C	5	0.000	0.000	0.00	0.000	0.00
6-9m	AUT80	C	5	0.000	0.000	0.00	0.000	0.00
6-9m	AUT80	E	5	0.000	0.000	0.00	0.000	0.00
6-9m	SPR81	C	5	0.000	0.000	0.00	0.000	0.00
6-9m	SPR81	E	5	30.700	0.440	0.44	1.800	2.60
6-9m	SUM81	C	5	0.000	0.000	0.00	0.000	0.00
6-9m	SUM81	E	5	31.200	0.440	0.44	1.800	3.20
6-9m	SPR82	C	5	0.000	0.000	0.00	0.000	0.00
6-9m	SPR82	E	5	11.300	0.350	0.35	1.200	0.80
6-9m	SUM82	C	10	0.000	0.000	0.00	0.000	0.00
6-9m	SUM82	E	10	66.400	0.730	0.31	4.400	2.80
6-9m	SUM82	Q	5	0.000	0.000	0.00	0.000	0.00

Appendix A, Continued

Species=*ALARIA ESCULENTA*

Depth range	Sample period	T	N	Arithmetic Mean	Mean of log transformed data	Standard error (log_{10})	Geometric Mean	Percent of biomass
0-2m	SUM79	C	5	1283.500	2.790	0.30	615.600	54.20
0-2m	SUM79	E	5	153.100	1.520	0.35	32.100	6.80
0-2m	SPR80	C	5	1887.000	3.090	0.21	1229.300	59.70
0-2m	AUT80	C	4	1745.000	3.230	0.06	1697.200	45.30
0-2m	AUT80	E	5	1190.000	3.030	0.10	1070.500	52.30
0-2m	SPR81	E	3	2799.000	3.400	0.16	2510.900	76.20
0-2m	SUM81	C	5	6078.000	2.840	0.79	690.800	99.90
0-2m	SUM81	E	5	5326.200	3.640	0.15	4364.200	98.10
0-2m	SUM82	C	10	5956.900	3.210	0.42	1620.800	97.40
0-2m	SUM82	E	10	5603.400	3.470	0.23	2950.200	99.90
2-3m	SUM79	C	5	1.600	0.190	0.19	0.500	9.10
2-3m	SUM79	E	5	0.100	0.030	0.03	0.100	8.60
2-3m	AUT79	C	3	0.000	0.000	0.00	0.000	0.00
2-3m	SPR80	C	5	0.000	0.000	0.00	0.000	0.00
2-3m	AUT80	E	5	0.000	0.000	0.00	0.000	0.00
2-3m	SPR81	C	5	105.100	1.110	0.48	11.900	77.50
2-3m	SPR81	E	5	1796.600	3.170	0.13	1478.100	75.90
2-3m	SUM81	C	5	0.200	0.050	0.05	0.100	0.00
2-3m	SUM81	E	6	1226.500	2.960	0.16	911.000	51.30
2-3m	SPR82	C	5	+	.	.	.	0.00
2-3m	SPR82	E	6	7061.900	3.520	0.36	3310.300	99.50
2-3m	SPR82	Q	5	841.100	2.850	0.14	706.900	85.10
2-3m	SUM82	C	10	4.100	0.270	0.16	0.900	0.60
2-3m	SUM82	E	10	2485.300	2.680	0.33	477.600	98.50
2-3m	SUM82	Q	5	2261.700	2.270	0.74	185.200	94.30
6-9m	SUM79	C	5	0.000	0.000	0.00	0.000	0.00
6-9m	SUM79	E	5	0.000	0.000	0.00	0.000	0.00
6-9m	AUT79	C	4	0.000	0.000	0.00	0.000	0.00
6-9m	SPR80	C	5	0.000	0.000	0.00	0.000	0.00
6-9m	AUT80	C	5	0.000	0.000	0.00	0.000	0.00
6-9m	AUT80	E	5	0.000	0.000	0.00	0.000	0.00
6-9m	SPR81	C	5	0.000	0.000	0.00	0.000	0.00
6-9m	SPR81	E	5	1.800	0.200	0.20	0.600	0.10
6-9m	SUM81	C	5	0.000	0.000	0.00	0.000	0.00
6-9m	SUM81	E	5	13.400	0.620	0.33	3.200	1.40
6-9m	SPR82	C	5	0.000	0.000	0.00	0.000	0.00
6-9m	SPR82	E	5	26.100	0.550	0.41	2.500	2.00
6-9m	SUM82	C	10	0.000	0.000	0.00	0.000	0.00
6-9m	SUM82	E	10	128.900	0.580	0.37	2.800	5.50
6-9m	SUM82	Q	5	107.700	0.580	0.54	2.800	14.50

Appendix A, Continued

Species=*ANTITHAMNIONELLA FLOCCOSA*

Depth range	Sample period	T	N	Arithmetic Mean	Mean of log transformed data	Standard error (log_{10})	Geometric Mean	Percent of biomass
0-2m	SUM79	C	5	0.000	0.000	0.00	0.000	0.00
0-2m	SUM79	E	5	0.000	0.000	0.00	0.000	0.00
0-2m	SPR80	C	5	0.000	0.000	0.00	0.000	0.00
0-2m	AUT80	C	4	0.000	0.000	0.00	0.000	0.00
0-2m	AUT80	E	5	0.000	+	0.01	0.000	0.00
0-2m	SPR81	E	3	0.000	0.000	0.00	0.000	0.00
0-2m	SUM81	C	5	0.000	0.000	0.00	0.000	0.00
0-2m	SUM81	E	5	0.000	0.000	0.00	0.000	0.00
0-2m	SUM82	C	9	0.000	0.000	0.00	0.000	0.00
0-2m	SUM82	E	10	0.000	0.000	0.00	0.000	0.00
2-3m	SUM79	C	5	+	.	.	.	0.00
2-3m	SUM79	E	5	0.000	0.000	0.00	0.000	0.00
2-3m	AUT79	C	3	+	.	.	.	0.00
2-3m	SPR80	C	5	0.000	0.000	0.00	0.000	0.00
2-3m	AUT80	E	5	0.000	0.020	0.01	0.000	0.10
2-3m	SPR81	C	5	0.000	0.000	0.00	0.000	0.00
2-3m	SPR81	E	5	0.000	0.000	0.00	0.000	0.00
2-3m	SUM81	C	5	0.000	0.000	0.00	0.000	0.00
2-3m	SUM81	E	6	0.000	0.000	0.00	0.000	0.00
2-3m	SPR82	C	5	0.000	0.000	0.00	0.000	0.00
2-3m	SPR82	E	6	0.000	0.000	0.00	0.000	0.00
2-3m	SPR82	Q	5	0.300	0.080	0.08	0.200	0.00
2-3m	SUM82	C	9	0.000	0.000	0.00	0.000	0.00
2-3m	SUM82	E	9	+	.	.	.	0.00
2-3m	SUM82	Q	4	0.000	0.000	0.00	0.000	0.00
6-9m	SUM79	C	5	+	.	.	.	0.00
6-9m	SUM79	E	5	0.000	0.000	0.00	0.000	0.00
6-9m	AUT79	C	4	0.000	0.000	0.00	0.000	0.00
6-9m	SPR80	C	5	0.000	0.000	0.00	0.000	0.00
6-9m	AUT80	C	5	+	.	.	.	0.00
6-9m	AUT80	E	5	+	.	.	.	0.00
6-9m	SPR81	C	5	0.000	0.000	0.00	0.000	0.00
6-9m	SPR81	E	5	0.000	0.000	0.00	0.000	0.00
6-9m	SUM81	C	5	0.000	0.000	0.00	0.000	0.00
6-9m	SUM81	E	5	0.000	0.000	0.00	0.000	0.00
6-9m	SPR82	C	5	0.000	0.000	0.00	0.000	0.00
6-9m	SPR82	E	5	0.000	0.000	0.00	0.000	0.00
6-9m	SUM82	C	9	0.000	0.000	0.00	0.000	0.00
6-9m	SUM82	E	9	0.000	0.000	0.00	0.000	0.00
6-9m	SUM82	Q	4	0.000	0.000	0.00	0.000	0.00

Appendix A, Continued

Species=*BONNEMAISONIA HAMIFERA*

Depth range	Sample period	T	N	Arithmetic Mean	Mean of log transformed data	Standard error (log_{10})	Geometric Mean	Percent of biomass
0-2m	SUM79	C	5	0.000	0.000	0.00	0.000	0.00
0-2m	SUM79	E	5	0.000	0.000	0.00	0.000	0.00
0-2m	SPR80	C	5	0.000	0.000	0.00	0.000	0.00
0-2m	AUT80	C	4	0.000	0.000	0.00	0.000	0.00
0-2m	AUT80	E	5	0.000	0.000	0.00	0.000	0.00
0-2m	SPR81	E	3	0.000	0.000	0.00	0.000	0.00
0-2m	SUM81	C	5	0.000	0.000	0.00	0.000	0.00
0-2m	SUM81	E	5	0.000	0.000	0.00	0.000	0.00
0-2m	SUM82	C	10	0.000	0.000	0.00	0.000	0.00
0-2m	SUM82	E	10	0.000	0.000	0.00	0.000	0.00
2-3m	SUM79	C	5	0.000	0.000	0.00	0.000	0.00
2-3m	SUM79	E	5	0.000	0.000	0.00	0.000	0.00
2-3m	AUT79	C	3	0.000	0.000	0.00	0.000	0.00
2-3m	SPR80	C	5	0.000	0.000	0.00	0.000	0.00
2-3m	AUT80	E	5	0.000	0.000	0.00	0.000	0.00
2-3m	SPR81	C	5	0.000	0.000	0.00	0.000	0.00
2-3m	SPR81	E	5	0.000	0.000	0.00	0.000	0.00
2-3m	SUM81	C	5	0.000	0.000	0.00	0.000	0.00
2-3m	SUM81	E	6	0.000	0.000	0.00	0.000	0.00
2-3m	SPR82	C	5	0.000	0.000	0.00	0.000	0.00
2-3m	SPR82	E	6	0.000	0.000	0.00	0.000	0.00
2-3m	SPR82	Q	5	0.000	0.000	0.00	0.000	0.00
2-3m	SUM82	C	10	0.000	0.000	0.00	0.000	0.00
2-3m	SUM82	E	10	0.000	0.000	0.00	0.000	0.00
2-3m	SUM82	Q	5	0.000	0.000	0.00	0.000	0.00
6-9m	SUM79	C	5	0.000	0.000	0.00	0.000	0.00
6-9m	SUM79	E	5	0.000	0.000	0.00	0.000	0.00
6-9m	AUT79	C	4	0.000	0.000	0.00	0.000	0.00
6-9m	SPR80	C	5	0.000	0.000	0.00	0.000	0.00
6-9m	AUT80	C	5	0.100	0.030	0.03	0.100	79.60
6-9m	AUT80	E	5	0.000	0.000	0.00	0.000	0.00
6-9m	SPR81	C	5	0.000	0.000	0.00	0.000	0.00
6-9m	SPR81	E	5	0.000	0.000	0.00	0.000	0.00
6-9m	SUM81	C	5	0.000	0.000	0.00	0.000	0.00
6-9m	SUM81	E	5	0.000	0.000	0.00	0.000	0.00
6-9m	SPR82	C	5	0.000	0.000	0.00	0.000	0.00
6-9m	SPR82	E	5	0.000	0.000	0.00	0.000	0.00
6-9m	SUM82	C	10	0.000	0.000	0.00	0.000	0.00
6-9m	SUM82	E	10	0.000	0.000	0.00	0.000	0.00
6-9m	SUM82	Q	5	0.000	0.000	0.00	0.000	0.00

Appendix A, Continued

Species=*CALLOPHYLLIS CRISTATA*

Depth range	Sample period	T	N	Arithmetic Mean	Mean of log transformed data	Standard error (log_{10})	Geometric Mean	Percent of biomass
0-2m	SUM79	C	5	0.000	0.000	0.00	0.000	0.00
0-2m	SUM79	E	5	0.000	0.000	0.00	0.000	0.00
0-2m	SPR80	C	5	0.000	0.000	0.00	0.000	0.00
0-2m	AUT80	C	4	0.000	0.000	0.00	0.000	0.00
0-2m	AUT80	E	5	0.000	0.000	0.00	0.000	0.00
0-2m	SPR81	E	3	0.000	0.000	0.00	0.000	0.00
0-2m	SUM81	C	5	0.000	0.000	0.00	0.000	0.00
0-2m	SUM81	E	5	0.000	0.000	0.00	0.000	0.00
0-2m	SUM82	C	10	0.000	0.000	0.00	0.000	0.00
0-2m	SUM82	E	10	0.000	0.000	0.00	0.000	0.00
2-3m	SUM79	C	5	0.000	0.000	0.00	0.000	0.00
2-3m	SUM79	E	5	0.000	0.000	0.00	0.000	0.00
2-3m	AUT79	C	3	0.000	0.000	0.00	0.000	0.00
2-3m	SPR80	C	5	0.000	0.000	0.00	0.000	0.00
2-3m	AUT80	E	5	0.000	0.000	0.00	0.000	0.00
2-3m	SPR81	C	5	0.000	0.000	0.00	0.000	0.00
2-3m	SPR81	E	5	0.000	0.000	0.00	0.000	0.00
2-3m	SUM81	C	5	0.000	0.000	0.00	0.000	0.00
2-3m	SUM81	E	6	0.000	0.000	0.00	0.000	0.00
2-3m	SPR82	C	5	0.000	0.000	0.00	0.000	0.00
2-3m	SPR82	E	6	0.000	0.000	0.00	0.000	0.00
2-3m	SPR82	Q	5	0.000	0.000	0.00	0.000	0.00
2-3m	SUM82	C	10	0.000	0.000	0.00	0.000	0.00
2-3m	SUM82	E	10	+	.	.	.	0.00
2-3m	SUM82	Q	5	0.000	0.000	0.00	0.000	0.00
6-9m	SUM79	C	5	0.000	0.000	0.00	0.000	0.00
6-9m	SUM79	E	5	0.000	0.000	0.00	0.000	0.00
6-9m	AUT79	C	4	0.000	0.000	0.00	0.000	0.00
6-9m	SPR80	C	5	0.000	0.000	0.00	0.000	0.00
6-9m	AUT80	C	5	0.000	0.000	0.00	0.000	0.00
6-9m	AUT80	E	5	0.000	0.000	0.00	0.000	0.00
6-9m	SPR81	C	5	0.000	0.000	0.00	0.000	0.00
6-9m	SPR81	E	5	0.000	+	0.01	0.000	0.00
6-9m	SUM81	C	5	0.000	0.000	0.00	0.000	0.00
6-9m	SUM81	E	5	0.000	0.020	0.02	0.000	0.00
6-9m	SPR82	C	5	0.000	0.000	0.00	0.000	0.00
6-9m	SPR82	E	5	0.000	0.000	0.00	0.000	0.00
6-9m	SUM82	C	10	0.000	0.000	0.00	0.000	0.00
6-9m	SUM82	E	10	+	.	.	.	0.00
6-9m	SUM82	Q	5	0.000	0.000	0.00	0.000	0.00

Appendix A, Continued

Species=*CERAMIUM RUBRUM*

Depth range	Sample period	T	N	Arithmetic Mean	Mean of log transformed data	Standard error (log_{10})	Geometric Mean	Percent of biomass
0-2m	SUM79	C	5	0.300	0.080	0.07	0.200	0.00
0-2m	SUM79	E	5	+	.	.	.	0.00
0-2m	SPR80	C	5	0.000	+	0.01	0.000	0.00
0-2m	AUT80	C	4	0.000	+	0.01	0.000	0.00
0-2m	AUT80	E	5	0.100	0.030	0.02	0.100	0.00
0-2m	SPR81	E	3	23.700	0.630	0.61	3.300	0.60
0-2m	SUM81	C	5	0.000	0.000	0.00	0.000	0.00
0-2m	SUM81	E	5	0.300	0.080	0.08	0.200	0.00
0-2m	SUM82	C	10	+	.	.	.	0.00
0-2m	SUM82	E	10	+	.	.	.	0.00
2-3m	SUM79	C	5	0.200	0.060	0.05	0.100	1.00
2-3m	SUM79	E	5	0.000	0.000	0.00	0.000	0.00
2-3m	AUT79	C	3	0.000	0.000	0.00	0.000	0.00
2-3m	SPR80	C	5	0.000	0.000	0.00	0.000	0.00
2-3m	AUT80	E	5	4.000	0.570	0.18	2.700	12.10
2-3m	SPR81	C	5	0.000	0.000	0.00	0.000	0.00
2-3m	SPR81	E	5	10.400	0.750	0.27	4.600	0.40
2-3m	SUM81	C	5	0.000	0.000	0.00	0.000	0.00
2-3m	SUM81	E	6	15.800	0.950	0.26	7.900	0.70
2-3m	SPR82	C	5	0.000	0.000	0.00	0.000	0.00
2-3m	SPR82	E	6	35.500	1.100	0.36	11.600	0.50
2-3m	SPR82	Q	5	+	.	.	.	0.00
2-3m	SUM82	C	10	+	.	.	.	0.00
2-3m	SUM82	E	10	6.100	0.380	0.19	1.400	0.20
2-3m	SUM82	Q	5	0.000	+	0.01	0.000	0.00
6-9m	SUM79	C	5	0.000	0.000	0.00	0.000	0.00
6-9m	SUM79	E	5	0.000	0.000	0.00	0.000	0.00
6-9m	AUT79	C	4	0.000	0.000	0.00	0.000	0.00
6-9m	SPR80	C	5	0.000	0.000	0.00	0.000	0.00
6-9m	AUT80	C	5	0.000	0.000	0.00	0.000	0.00
6-9m	AUT80	E	5	0.500	0.150	0.07	0.400	2.10
6-9m	SPR81	C	5	0.000	0.000	0.00	0.000	0.00
6-9m	SPR81	E	5	0.500	0.110	0.11	0.300	0.00
6-9m	SUM81	C	5	0.000	0.000	0.00	0.000	0.00
6-9m	SUM81	E	5	+	.	.	.	0.00
6-9m	SPR82	C	5	0.000	0.000	0.00	0.000	0.00
6-9m	SPR82	E	5	9.700	0.400	0.33	1.500	0.70
6-9m	SUM82	C	10	0.000	0.000	0.00	0.000	0.00
6-9m	SUM82	E	10	5.800	0.230	0.18	0.700	0.20
6-9m	SUM82	Q	5	+	.	.	.	0.00

Appendix A, Continued

Species=*CHORDA TOMENTOSA*

Depth range	Sample period	T	N	Arithmetic Mean	Mean of log transformed data	Standard error (log_{10})	Geometric Mean	Percent of biomass
0-2m	SUM79	C	5	0.000	0.000	0.00	0.000	0.00
0-2m	SUM79	E	5	1.200	0.170	0.17	0.500	0.10
0-2m	SPR80	C	5	12.400	0.580	0.33	2.800	0.40
0-2m	AUT80	C	4	0.000	0.000	0.00	0.000	0.00
0-2m	AUT80	E	5	0.000	0.000	0.00	0.000	0.00
0-2m	SPR81	E	3	0.000	0.000	0.00	0.000	0.00
0-2m	SUM81	C	5	0.000	0.000	0.00	0.000	0.00
0-2m	SUM81	E	5	0.000	0.000	0.00	0.000	0.00
0-2m	SUM82	C	10	0.000	0.000	0.00	0.000	0.00
0-2m	SUM82	E	10	0.000	0.000	0.00	0.000	0.00
2-3m	SUM79	C	5	0.000	0.000	0.00	0.000	0.00
2-3m	SUM79	E	5	0.000	0.000	0.00	0.000	0.00
2-3m	AUT79	C	3	0.000	0.000	0.00	0.000	0.00
2-3m	SPR80	C	5	0.000	0.000	0.00	0.000	0.00
2-3m	AUT80	E	5	0.000	0.000	0.00	0.000	0.00
2-3m	SPR81	C	5	0.000	0.000	0.00	0.000	0.00
2-3m	SPR81	E	5	1.600	0.200	0.19	0.600	0.10
2-3m	SUM81	C	5	0.000	0.000	0.00	0.000	0.00
2-3m	SUM81	E	6	0.000	0.000	0.00	0.000	0.00
2-3m	SPR82	C	5	0.000	0.000	0.00	0.000	0.00
2-3m	SPR82	E	6	+	.	.	.	0.00
2-3m	SPR82	Q	5	0.000	0.000	0.00	0.000	0.00
2-3m	SUM82	C	10	28.000	0.240	0.24	0.700	4.20
2-3m	SUM82	E	10	21.200	0.230	0.23	0.700	0.80
2-3m	SUM82	Q	5	0.000	0.000	0.00	0.000	0.00
6-9m	SUM79	C	5	0.000	0.000	0.00	0.000	0.00
6-9m	SUM79	E	5	0.000	0.000	0.00	0.000	0.00
6-9m	AUT79	C	4	0.000	0.000	0.00	0.000	0.00
6-9m	SPR80	C	5	0.000	0.000	0.00	0.000	0.00
6-9m	AUT80	C	5	0.000	0.000	0.00	0.000	0.00
6-9m	AUT80	E	5	0.000	0.000	0.00	0.000	0.00
6-9m	SPR81	C	5	0.000	0.000	0.00	0.000	0.00
6-9m	SPR81	E	5	0.000	0.000	0.00	0.000	0.00
6-9m	SUM81	C	5	0.000	0.000	0.00	0.000	0.00
6-9m	SUM81	E	5	1.100	0.160	0.16	0.400	0.10
6-9m	SPR82	C	5	0.000	0.000	0.00	0.000	0.00
6-9m	SPR82	E	5	0.000	0.000	0.00	0.000	0.00
6-9m	SUM82	C	10	0.000	0.000	0.00	0.000	0.00
6-9m	SUM82	E	10	0.000	0.000	0.00	0.000	0.00
6-9m	SUM82	Q	5	0.000	0.000	0.00	0.000	0.00

Appendix A, Continued

Species=*CHORDARIA FLAGELLIFORMIS*

Depth range	Sample period	T	N	Arithmetic Mean	Mean of log transformed data	Standard error ($\log_{10}$)	Geometric Mean	Percent of biomass
0-2m	SUM79	C	5	749.300	2.650	0.32	445.700	31.70
0-2m	SUM79	E	5	1909.400	3.250	0.08	1777.300	84.80
0-2m	SPR80	C	5	43.900	1.110	0.39	11.900	1.40
0-2m	AUT80	C	4	149.000	0.950	0.63	7.900	3.90
0-2m	AUT80	E	5	94.700	1.530	0.36	32.900	4.20
0-2m	SPR81	E	3	8.600	0.590	0.42	2.900	0.20
0-2m	SUM81	C	5	0.000	0.000	0.00	0.000	0.00
0-2m	SUM81	E	5	+	.	.	.	0.00
0-2m	SUM82	C	10	28.600	0.490	0.27	2.100	0.50
0-2m	SUM82	E	10	+	.	.	.	0.00
2-3m	SUM79	C	5	11.200	0.590	0.35	2.900	63.80
2-3m	SUM79	E	5	0.700	0.130	0.13	0.300	73.80
2-3m	AUT79	C	3	0.000	0.000	0.00	0.000	0.00
2-3m	SPR80	C	5	0.000	0.000	0.00	0.000	0.00
2-3m	AUT80	E	5	1.300	0.320	0.08	1.100	3.90
2-3m	SPR81	C	5	1.900	0.290	0.18	0.900	1.40
2-3m	SPR81	E	5	0.300	0.100	0.05	0.300	0.00
2-3m	SUM81	C	5	9.800	0.760	0.25	4.800	1.50
2-3m	SUM81	E	6	57.600	0.660	0.41	3.600	2.40
2-3m	SPR82	C	5	+	.	.	.	0.00
2-3m	SPR82	E	6	0.000	0.000	0.00	0.000	0.00
2-3m	SPR82	Q	5	0.000	0.000	0.00	0.000	0.00
2-3m	SUM82	C	10	46.200	1.250	0.22	16.800	6.90
2-3m	SUM82	E	10	5.900	0.240	0.18	0.700	0.20
2-3m	SUM82	Q	5	1.700	0.190	0.19	0.500	0.10
6-9m	SUM79	C	5	0.900	0.150	0.14	0.400	3.50
6-9m	SUM79	E	5	0.000	0.000	0.00	0.000	0.00
6-9m	AUT79	C	4	0.000	0.000	0.00	0.000	0.00
6-9m	SPR80	C	5	0.000	0.000	0.00	0.000	0.00
6-9m	AUT80	C	5	0.000	0.000	0.00	0.000	0.00
6-9m	AUT80	E	5	3.000	0.410	0.21	1.600	13.00
6-9m	SPR81	C	5	0.000	0.000	0.00	0.000	0.00
6-9m	SPR81	E	5	0.400	0.110	0.07	0.300	0.00
6-9m	SUM81	C	5	0.000	0.000	0.00	0.000	0.00
6-9m	SUM81	E	5	43.000	1.580	0.13	37.000	4.40
6-9m	SPR82	C	5	0.000	0.000	0.00	0.000	0.00
6-9m	SPR82	E	5	13.400	0.370	0.37	1.300	1.00
6-9m	SUM82	C	10	1.700	0.250	0.12	0.800	0.30
6-9m	SUM82	E	10	8.900	0.430	0.20	1.700	0.40
6-9m	SUM82	Q	5	16.700	0.390	0.39	1.500	2.30

Appendix A, Continued

Species=*CYSTOCLONIUM PURPUREUM*

Depth range	Sample period	T	N	Arithmetic Mean	Mean of log transformed data	Standard error (log_{10})	Geometric Mean	Percent of biomass
0-2m	SUM79	C	5	0.000	0.000	0.00	0.000	0.00
0-2m	SUM79	E	5	0.000	0.000	0.00	0.000	0.00
0-2m	SPR80	C	5	0.000	0.000	0.00	0.000	0.00
0-2m	AUT80	C	4	0.000	0.000	0.00	0.000	0.00
0-2m	AUT80	E	5	0.100	0.050	0.05	0.100	0.00
0-2m	SPR81	E	3	0.000	0.000	0.00	0.000	0.00
0-2m	SUM81	C	5	0.000	0.000	0.00	0.000	0.00
0-2m	SUM81	E	5	0.000	0.000	0.00	0.000	0.00
0-2m	SUM82	C	10	0.000	0.000	0.00	0.000	0.00
0-2m	SUM82	E	10	0.000	0.000	0.00	0.000	0.00
2-3m	SUM79	C	5	0.000	0.000	0.00	0.000	0.00
2-3m	SUM79	E	5	0.000	0.000	0.00	0.000	0.00
2-3m	AUT79	C	3	0.000	0.000	0.00	0.000	0.00
2-3m	SPR80	C	5	0.000	0.000	0.00	0.000	0.00
2-3m	AUT80	E	5	0.300	0.070	0.07	0.200	0.80
2-3m	SPR81	C	5	0.000	0.000	0.00	0.000	0.00
2-3m	SPR81	E	5	0.000	0.000	0.00	0.000	0.00
2-3m	SUM81	C	5	0.100	0.020	0.02	0.000	0.00
2-3m	SUM81	E	6	0.000	0.000	0.00	0.000	0.00
2-3m	SPR82	C	5	0.000	0.000	0.00	0.000	0.00
2-3m	SPR82	E	6	0.000	0.000	0.00	0.000	0.00
2-3m	SPR82	Q	5	0.000	0.000	0.00	0.000	0.00
2-3m	SUM82	C	10	0.000	0.000	0.00	0.000	0.00
2-3m	SUM82	E	10	0.000	0.000	0.00	0.000	0.00
2-3m	SUM82	Q	5	0.000	0.000	0.00	0.000	0.00
6-9m	SUM79	C	5	0.000	0.000	0.00	0.000	0.00
6-9m	SUM79	E	5	0.000	0.000	0.00	0.000	0.00
6-9m	AUT79	C	4	0.000	0.000	0.00	0.000	0.00
6-9m	SPR80	C	5	0.000	0.000	0.00	0.000	0.00
6-9m	AUT80	C	5	0.000	0.000	0.00	0.000	0.00
6-9m	AUT80	E	5	0.000	0.000	0.00	0.000	0.00
6-9m	SPR81	C	5	0.000	0.000	0.00	0.000	0.00
6-9m	SPR81	E	5	0.000	0.000	0.00	0.000	0.00
6-9m	SUM81	C	5	0.000	0.000	0.00	0.000	0.00
6-9m	SUM81	E	5	0.000	0.000	0.00	0.000	0.00
6-9m	SPR82	C	5	0.000	0.000	0.00	0.000	0.00
6-9m	SPR82	E	5	0.000	0.000	0.00	0.000	0.00
6-9m	SUM82	C	10	0.000	0.000	0.00	0.000	0.00
6-9m	SUM82	E	10	0.000	0.000	0.00	0.000	0.00
6-9m	SUM82	Q	5	0.000	0.000	0.00	0.000	0.00

Appendix A, Continued

Species=*DERBESIA MARINA*

Depth range	Sample period	T	N	Arithmetic Mean	Mean of log transformed data	Standard error (log_{10})	Geometric Mean	Percent of biomass
0-2m	SUM79	C	5	0.000	0.000	0.00	0.000	0.00
0-2m	SUM79	E	5	0.000	0.000	0.00	0.000	0.00
0-2m	SPR80	C	5	0.000	0.000	0.00	0.000	0.00
0-2m	AUT80	C	4	0.000	0.000	0.00	0.000	0.00
0-2m	AUT80	E	5	0.000	0.000	0.00	0.000	0.00
0-2m	SPR81	E	3	0.000	0.000	0.00	0.000	0.00
0-2m	SUM81	C	5	0.000	0.000	0.00	0.000	0.00
0-2m	SUM81	E	5	0.000	0.000	0.00	0.000	0.00
0-2m	SUM82	C	10	0.000	0.000	0.00	0.000	0.00
0-2m	SUM82	E	10	0.000	0.000	0.00	0.000	0.00
2-3m	SUM79	C	5	+	.	.	.	0.00
2-3m	SUM79	E	5	+	.	.	.	0.00
2-3m	AUT79	C	3	0.000	0.000	0.00	0.000	0.00
2-3m	SPR80	C	5	+	.	.	.	0.00
2-3m	AUT80	E	5	0.100	0.040	0.04	0.100	0.40
2-3m	SPR81	C	5	0.600	0.120	0.12	0.300	0.40
2-3m	SPR81	E	5	0.000	0.000	0.00	0.000	0.00
2-3m	SUM81	C	5	0.000	0.000	0.00	0.000	0.00
2-3m	SUM81	E	6	0.000	0.000	0.00	0.000	0.00
2-3m	SPR82	C	5	0.000	0.000	0.00	0.000	0.00
2-3m	SPR82	E	6	0.000	0.000	0.00	0.000	0.00
2-3m	SPR82	Q	5	0.000	0.000	0.00	0.000	0.00
2-3m	SUM82	C	10	0.000	0.000	0.00	0.000	0.00
2-3m	SUM82	E	10	0.000	0.000	0.00	0.000	0.00
2-3m	SUM82	Q	5	0.000	0.000	0.00	0.000	0.00
6-9m	SUM79	C	5	+	.	.	.	0.00
6-9m	SUM79	E	5	+	.	.	.	0.00
6-9m	AUT79	C	4	0.000	0.000	0.00	0.000	0.00
6-9m	SPR80	C	5	0.000	0.000	0.00	0.000	0.00
6-9m	AUT80	C	5	0.000	0.000	0.00	0.000	0.00
6-9m	AUT80	E	5	0.000	0.000	0.00	0.000	0.00
6-9m	SPR81	C	5	0.000	0.000	0.00	0.000	0.00
6-9m	SPR81	E	5	0.000	0.000	0.00	0.000	0.00
6-9m	SUM81	C	5	0.000	0.000	0.00	0.000	0.00
6-9m	SUM81	E	5	0.000	0.000	0.00	0.000	0.00
6-9m	SPR82	C	5	0.000	0.000	0.00	0.000	0.00
6-9m	SPR82	E	5	0.000	0.000	0.00	0.000	0.00
6-9m	SUM82	C	10	0.000	0.000	0.00	0.000	0.00
6-9m	SUM82	E	10	0.000	0.000	0.00	0.000	0.00
6-9m	SUM82	Q	5	0.000	0.000	0.00	0.000	0.00

Appendix A, Continued

Species=*DESMARESTIA SPP.*

Depth range	Sample period	T	N	Arithmetic Mean	Mean of log transformed data	Standard error (log_{10})	Geometric Mean	Percent of biomass
0-2m	SUM79	C	5	2.000	0.210	0.21	0.600	0.10
0-2m	SUM79	E	5	0.000	0.000	0.00	0.000	0.00
0-2m	SPR80	C	5	0.000	0.000	0.00	0.000	0.00
0-2m	AUT80	C	4	0.000	0.000	0.00	0.000	0.00
0-2m	AUT80	E	5	0.000	0.000	0.00	0.000	0.00
0-2m	SPR81	E	3	77.600	0.850	0.76	6.100	2.10
0-2m	SUM81	C	5	0.000	0.000	0.00	0.000	0.00
0-2m	SUM81	E	5	0.000	0.000	0.00	0.000	0.00
0-2m	SUM82	C	10	4.800	0.170	0.17	0.500	0.10
0-2m	SUM82	E	10	0.000	0.000	0.00	0.000	0.00
2-3m	SUM79	C	5	0.200	0.060	0.06	0.100	1.20
2-3m	SUM79	E	5	0.000	0.020	0.02	0.000	5.00
2-3m	AUT79	C	3	0.000	0.000	0.00	0.000	0.00
2-3m	SPR80	C	5	0.000	0.000	0.00	0.000	0.00
2-3m	AUT80	E	5	0.000	0.000	0.00	0.000	0.00
2-3m	SPR81	C	5	18.500	0.620	0.40	3.200	13.70
2-3m	SPR81	E	5	48.600	1.440	0.26	26.500	2.10
2-3m	SUM81	C	5	605.800	1.400	0.73	24.100	94.00
2-3m	SUM81	E	6	679.500	2.230	0.38	168.800	28.40
2-3m	SPR82	C	5	+	.	.	.	0.00
2-3m	SPR82	E	6	0.000	0.000	0.00	0.000	0.00
2-3m	SPR82	Q	5	41.900	0.990	0.44	8.800	4.20
2-3m	SUM82	C	10	304.300	1.130	0.32	12.500	45.50
2-3m	SUM82	E	10	0.400	0.070	0.07	0.200	0.00
2-3m	SUM82	Q	5	53.000	1.180	0.43	14.100	2.20
6-9m	SUM79	C	5	0.900	0.170	0.14	0.500	3.90
6-9m	SUM79	E	5	0.000	0.000	0.00	0.000	0.00
6-9m	AUT79	C	4	0.000	0.000	0.00	0.000	0.00
6-9m	SPR80	C	5	0.000	0.000	0.00	0.000	0.00
6-9m	AUT80	C	5	0.000	0.000	0.00	0.000	0.00
6-9m	AUT80	E	5	0.000	+	0.01	0.000	0.20
6-9m	SPR81	C	5	0.000	0.000	0.00	0.000	0.00
6-9m	SPR81	E	5	484.300	1.500	0.68	30.600	40.80
6-9m	SUM81	C	5	0.000	0.000	0.00	0.000	0.00
6-9m	SUM81	E	5	620.700	2.420	0.30	262.000	63.10
6-9m	SPR82	C	5	+	.	.	.	0.00
6-9m	SPR82	E	5	505.600	2.610	0.15	406.400	38.00
6-9m	SUM82	C	10	296.300	1.230	0.37	16.000	54.10
6-9m	SUM82	E	10	1895.000	1.950	0.50	88.100	80.30
6-9m	SUM82	Q	5	235.600	1.740	0.39	54.000	31.80

Appendix A, Continued

Species=*DICTYOSIPHON FOENICULACEUS*

Depth range	Sample period	T	N	Arithmetic Mean	Mean of log transformed data	Standard error (log_{10})	Geometric Mean	Percent of biomass
0-2m	SUM79	C	5	10.400	0.970	0.16	8.300	0.40
0-2m	SUM79	E	5	47.200	1.610	0.13	39.700	2.10
0-2m	SPR80	C	5	0.000	0.000	0.00	0.000	0.00
0-2m	AUT80	C	4	0.000	0.000	0.00	0.000	0.00
0-2m	AUT80	E	5	0.000	0.000	0.00	0.000	0.00
0-2m	SPR81	E	3	0.000	0.000	0.00	0.000	0.00
0-2m	SUM81	C	5	0.000	0.000	0.00	0.000	0.00
0-2m	SUM81	E	5	0.000	0.000	0.00	0.000	0.00
0-2m	SUM82	C	10	1.800	0.130	0.13	0.300	0.00
0-2m	SUM82	E	10	0.000	0.000	0.00	0.000	0.00
2-3m	SUM79	C	5	0.500	0.110	0.10	0.300	2.70
2-3m	SUM79	E	5	0.000	+	0.01	0.000	2.90
2-3m	AUT79	C	3	0.000	0.000	0.00	0.000	0.00
2-3m	SPR80	C	5	0.000	0.000	0.00	0.000	0.00
2-3m	AUT80	E	5	0.000	0.000	0.00	0.000	0.00
2-3m	SPR81	C	5	0.000	0.000	0.00	0.000	0.00
2-3m	SPR81	E	5	0.000	0.000	0.00	0.000	0.00
2-3m	SUM81	C	5	1.400	0.220	0.16	0.700	0.20
2-3m	SUM81	E	6	5.000	0.250	0.25	0.800	0.20
2-3m	SPR82	C	5	0.000	0.000	0.00	0.000	0.00
2-3m	SPR82	E	6	0.000	0.000	0.00	0.000	0.00
2-3m	SPR82	Q	5	0.000	0.000	0.00	0.000	0.00
2-3m	SUM82	C	10	9.300	0.580	0.20	2.800	1.40
2-3m	SUM82	E	10	0.100	0.040	0.04	0.100	0.00
2-3m	SUM82	Q	5	0.000	0.000	0.00	0.000	0.00
6-9m	SUM79	C	5	0.000	0.020	0.02	0.000	0.20
6-9m	SUM79	E	5	0.000	0.000	0.00	0.000	0.00
6-9m	AUT79	C	4	0.000	0.000	0.00	0.000	0.00
6-9m	SPR80	C	5	0.000	0.000	0.00	0.000	0.00
6-9m	AUT80	C	5	0.000	0.000	0.00	0.000	0.00
6-9m	AUT80	E	5	0.000	0.000	0.00	0.000	0.00
6-9m	SPR81	C	5	0.000	0.000	0.00	0.000	0.00
6-9m	SPR81	E	5	0.000	0.000	0.00	0.000	0.00
6-9m	SUM81	C	5	0.000	0.000	0.00	0.000	0.00
6-9m	SUM81	E	5	0.700	0.190	0.10	0.500	0.10
6-9m	SPR82	C	5	0.000	0.000	0.00	0.000	0.00
6-9m	SPR82	E	5	0.000	0.000	0.00	0.000	0.00
6-9m	SUM82	C	10	1.600	0.180	0.12	0.500	0.30
6-9m	SUM82	E	10	0.000	0.000	0.00	0.000	0.00
6-9m	SUM82	Q	5	+	.	.	.	0.00

Appendix A, Continued

Species=*ECTOCARPUS SPP.*

Depth range	Sample period	T	N	Arithmetic Mean	Mean of log transformed data	Standard error (log_{10})	Geometric Mean	Percent of biomass
0-2m	SUM79	C	5	0.400	0.120	0.05	0.300	0.00
0-2m	SUM79	E	5	3.400	0.440	0.21	1.800	0.20
0-2m	SPR80	C	5	0.200	0.070	0.05	0.200	0.00
0-2m	AUT80	C	4	34.300	1.030	0.46	9.700	0.90
0-2m	AUT80	E	5	51.500	1.280	0.38	18.100	2.30
0-2m	SPR81	E	3	0.100	0.040	0.04	0.100	0.00
0-2m	SUM81	C	5	0.300	0.070	0.07	0.200	0.00
0-2m	SUM81	E	5	0.000	0.000	0.00	0.000	0.00
0-2m	SUM82	C	10	25.500	0.680	0.25	3.800	0.40
0-2m	SUM82	E	10	+	.	.	.	0.00
2-3m	SUM79	C	5	0.300	0.090	0.08	0.200	1.90
2-3m	SUM79	E	5	0.000	+	0.01	0.000	2.70
2-3m	AUT79	C	3	0.000	0.000	0.00	0.000	0.00
2-3m	SPR80	C	5	+	.	.	.	0.00
2-3m	AUT80	E	5	0.000	0.000	0.00	0.000	0.00
2-3m	SPR81	C	5	0.000	0.000	0.00	0.000	0.00
2-3m	SPR81	E	5	0.000	0.000	0.00	0.000	0.00
2-3m	SUM81	C	5	10.900	0.600	0.31	3.000	1.70
2-3m	SUM81	E	6	1.300	0.150	0.15	0.400	0.10
2-3m	SPR82	C	5	0.000	0.000	0.00	0.000	0.00
2-3m	SPR82	E	6	0.100	0.030	0.03	0.100	0.00
2-3m	SPR82	Q	5	0.000	0.000	0.00	0.000	0.00
2-3m	SUM82	C	10	165.200	1.850	0.23	69.800	24.70
2-3m	SUM82	E	10	2.200	0.170	0.13	0.500	0.10
2-3m	SUM82	Q	5	59.000	0.780	0.49	5.000	2.50
6-9m	SUM79	C	5	+	.	.	.	0.00
6-9m	SUM79	E	5	+	.	.	.	0.00
6-9m	AUT79	C	4	+	.	.	.	0.00
6-9m	SPR80	C	5	+	.	.	.	0.00
6-9m	AUT80	C	5	+	.	.	.	0.00
6-9m	AUT80	E	5	0.100	0.030	0.02	0.100	0.30
6-9m	SPR81	C	5	0.000	+	0.01	0.000	16.70
6-9m	SPR81	E	5	0.000	+	0.01	0.000	0.00
6-9m	SUM81	C	5	2.800	0.240	0.24	0.700	99.90
6-9m	SUM81	E	5	50.800	1.300	0.33	19.000	5.20
6-9m	SPR82	C	5	0.000	0.000	0.00	0.000	0.00
6-9m	SPR82	E	5	+	.	.	.	0.00
6-9m	SUM82	C	10	164.500	1.700	0.30	49.100	30.10
6-9m	SUM82	E	10	3.700	0.320	0.15	1.100	0.20
6-9m	SUM82	Q	5	366.100	1.680	0.61	46.900	49.40

Appendix A, Continued

Species=*EUDESME VIRESCENS*

Depth range	Sample period	T	N	Arithmetic Mean	Mean of log transformed data	Standard error (log_{10})	Geometric Mean	Percent of biomass
0-2m	SUM79	C	5	0.000	0.000	0.00	0.000	0.00
0-2m	SUM79	E	5	0.000	0.000	0.00	0.000	0.00
0-2m	SPR80	C	5	0.000	0.000	0.00	0.000	0.00
0-2m	AUT80	C	4	0.000	0.000	0.00	0.000	0.00
0-2m	AUT80	E	5	0.000	0.000	0.00	0.000	0.00
0-2m	SPR81	E	3	0.000	0.000	0.00	0.000	0.00
0-2m	SUM81	C	5	0.000	0.000	0.00	0.000	0.00
0-2m	SUM81	E	5	0.000	0.000	0.00	0.000	0.00
0-2m	SUM82	C	10	0.000	0.000	0.00	0.000	0.00
0-2m	SUM82	E	10	0.000	0.000	0.00	0.000	0.00
2-3m	SUM79	C	5	0.000	0.000	0.00	0.000	0.00
2-3m	SUM79	E	5	0.000	0.000	0.00	0.000	0.00
2-3m	AUT79	C	3	0.000	0.000	0.00	0.000	0.00
2-3m	SPR80	C	5	0.000	0.000	0.00	0.000	0.00
2-3m	AUT80	E	5	0.000	0.000	0.00	0.000	0.00
2-3m	SPR81	C	5	0.200	0.060	0.04	0.100	0.10
2-3m	SPR81	E	5	0.000	0.000	0.00	0.000	0.00
2-3m	SUM81	C	5	8.300	0.670	0.29	3.700	1.30
2-3m	SUM81	E	6	0.000	0.000	0.00	0.000	0.00
2-3m	SPR82	C	5	+	.	.	.	0.00
2-3m	SPR82	E	6	0.000	0.000	0.00	0.000	0.00
2-3m	SPR82	Q	5	0.000	0.000	0.00	0.000	0.00
2-3m	SUM82	C	10	101.000	1.720	0.23	51.500	15.10
2-3m	SUM82	E	10	0.000	0.000	0.00	0.000	0.00
2-3m	SUM82	Q	5	0.900	0.180	0.14	0.500	0.00
6-9m	SUM79	C	5	20.500	0.580	0.39	2.800	84.80
6-9m	SUM79	E	5	0.000	0.000	0.00	0.000	0.00
6-9m	AUT79	C	4	0.000	0.000	0.00	0.000	0.00
6-9m	SPR80	C	5	0.000	0.000	0.00	0.000	0.00
6-9m	AUT80	C	5	0.000	0.000	0.00	0.000	0.00
6-9m	AUT80	E	5	0.000	0.000	0.00	0.000	0.00
6-9m	SPR81	C	5	0.000	0.000	0.00	0.000	0.00
6-9m	SPR81	E	5	0.000	0.000	0.00	0.000	0.00
6-9m	SUM81	C	5	0.000	0.000	0.00	0.000	0.00
6-9m	SUM81	E	5	18.000	0.630	0.40	3.300	1.80
6-9m	SPR82	C	5	0.000	0.000	0.00	0.000	0.00
6-9m	SPR82	E	5	0.000	0.000	0.00	0.000	0.00
6-9m	SUM82	C	10	78.400	1.440	0.28	26.500	14.30
6-9m	SUM82	E	10	0.300	0.080	0.05	0.200	0.00
6-9m	SUM82	Q	5	12.000	0.440	0.34	1.800	1.60

Appendix A, Continued

Species=*GIFFORDIA SPP.*

Depth range	Sample period	T	N	Arithmetic Mean	Mean of log transformed data	Standard error (log_{10})	Geometric Mean	Percent of biomass
0-2m	SUM79	C	5	0.000	0.000	0.00	0.000	0.00
0-2m	SUM79	E	5	+	.	.	.	0.00
0-2m	SPR80	C	5	0.000	0.000	0.00	0.000	0.00
0-2m	AUT80	C	4	0.000	0.000	0.00	0.000	0.00
0-2m	AUT80	E	5	0.000	0.000	0.00	0.000	0.00
0-2m	SPR81	E	3	0.000	0.000	0.00	0.000	0.00
0-2m	SUM81	C	5	0.000	0.000	0.00	0.000	0.00
0-2m	SUM81	E	5	0.000	0.000	0.00	0.000	0.00
0-2m	SUM82	C	10	+	.	.	.	0.00
0-2m	SUM82	E	10	0.000	0.000	0.00	0.000	0.00
2-3m	SUM79	C	5	0.500	0.110	0.11	0.300	2.90
2-3m	SUM79	E	5	+	.	.	.	0.00
2-3m	AUT79	C	3	0.000	0.000	0.00	0.000	0.00
2-3m	SPR80	C	5	0.000	0.000	0.00	0.000	0.00
2-3m	AUT80	E	5	0.000	0.000	0.00	0.000	0.00
2-3m	SPR81	C	5	2.800	0.370	0.22	1.300	2.10
2-3m	SPR81	E	5	0.000	+	0.01	0.000	0.00
2-3m	SUM81	C	5	0.000	0.000	0.00	0.000	0.00
2-3m	SUM81	E	6	0.000	0.000	0.00	0.000	0.00
2-3m	SPR82	C	5	+	.	.	.	0.00
2-3m	SPR82	E	6	0.000	0.000	0.00	0.000	0.00
2-3m	SPR82	Q	5	0.000	0.000	0.00	0.000	0.00
2-3m	SUM82	C	10	0.000	0.000	0.00	0.000	0.00
2-3m	SUM82	E	10	0.000	0.000	0.00	0.000	0.00
2-3m	SUM82	Q	5	0.000	0.000	0.00	0.000	0.00
6-9m	SUM79	C	5	+	.	.	.	0.00
6-9m	SUM79	E	5	0.000	0.000	0.00	0.000	0.00
6-9m	AUT79	C	4	0.000	0.000	0.00	0.000	0.00
6-9m	SPR80	C	5	0.000	0.000	0.00	0.000	0.00
6-9m	AUT80	C	5	0.000	0.000	0.00	0.000	0.00
6-9m	AUT80	E	5	0.000	0.000	0.00	0.000	0.00
6-9m	SPR81	C	5	0.000	0.000	0.00	0.000	0.00
6-9m	SPR81	E	5	0.000	0.000	0.00	0.000	0.00
6-9m	SUM81	C	5	0.000	0.000	0.00	0.000	0.00
6-9m	SUM81	E	5	0.100	0.050	0.05	0.100	0.00
6-9m	SPR82	C	5	+	.	.	.	0.00
6-9m	SPR82	E	5	0.000	0.000	0.00	0.000	0.00
6-9m	SUM82	C	10	0.000	0.000	0.00	0.000	0.00
6-9m	SUM82	E	10	0.000	0.000	0.00	0.000	0.00
6-9m	SUM82	Q	5	0.000	0.000	0.00	0.000	0.00

Appendix A, Continued

Species=*DEVALERAEA RAMENTACEA*

Depth range	Sample period	T	N	Arithmetic Mean	Mean of log transformed data	Standard error (log_{10})	Geometric Mean	Percent of biomass
0-2m	SUM79	C	5	199.700	1.580	0.49	37.000	8.40
0-2m	SUM79	E	5	39.100	1.110	0.41	11.900	1.70
0-2m	SPR80	C	5	357.200	1.220	0.63	15.600	11.30
0-2m	AUT80	C	4	44.200	1.150	0.41	13.100	1.10
0-2m	AUT80	E	5	103.800	1.540	0.45	33.700	4.60
0-2m	SPR81	E	3	0.400	0.160	0.02	0.400	0.00
0-2m	SUM81	C	5	1.200	0.170	0.17	0.500	0.00
0-2m	SUM81	E	5	15.800	0.580	0.38	2.800	0.30
0-2m	SUM82	C	10	0.900	0.150	0.09	0.400	0.00
0-2m	SUM82	E	10	0.300	0.070	0.06	0.200	0.00
2-3m	SUM79	C	5	0.000	+	0.01	0.000	0.20
2-3m	SUM79	E	5	0.000	0.000	0.00	0.000	0.00
2-3m	AUT79	C	3	0.000	0.000	0.00	0.000	0.00
2-3m	SPR80	C	5	0.000	0.000	0.00	0.000	0.00
2-3m	AUT80	E	5	+	.	.	.	0.00
2-3m	SPR81	C	5	2.700	0.260	0.22	0.800	2.00
2-3m	SPR81	E	5	0.000	+	0.01	0.000	0.00
2-3m	SUM81	C	5	0.000	0.000	0.00	0.000	0.00
2-3m	SUM81	E	6	0.000	0.000	0.00	0.000	0.00
2-3m	SPR82	C	5	+	.	.	.	0.00
2-3m	SPR82	E	6	0.000	0.000	0.00	0.000	0.00
2-3m	SPR82	Q	5	+	.	.	.	0.00
2-3m	SUM82	C	10	0.100	0.020	0.02	0.000	0.00
2-3m	SUM82	E	10	+	.	.	.	0.00
2-3m	SUM82	Q	5	0.000	0.000	0.00	0.000	0.00
6-9m	SUM79	C	5	0.000	0.000	0.00	0.000	0.00
6-9m	SUM79	E	5	0.000	0.000	0.00	0.000	0.00
6-9m	AUT79	C	4	0.000	0.000	0.00	0.000	0.00
6-9m	SPR80	C	5	0.000	0.000	0.00	0.000	0.00
6-9m	AUT80	C	5	0.000	0.000	0.00	0.000	0.00
6-9m	AUT80	E	5	0.000	0.000	0.00	0.000	0.00
6-9m	SPR81	C	5	0.000	0.000	0.00	0.000	0.00
6-9m	SPR81	E	5	0.000	0.000	0.00	0.000	0.00
6-9m	SUM81	C	5	0.000	0.000	0.00	0.000	0.00
6-9m	SUM81	E	5	0.000	0.000	0.00	0.000	0.00
6-9m	SPR82	C	5	0.000	0.000	0.00	0.000	0.00
6-9m	SPR82	E	5	0.000	0.000	0.00	0.000	0.00
6-9m	SUM82	C	10	0.000	0.000	0.00	0.000	0.00
6-9m	SUM82	E	10	0.000	0.000	0.00	0.000	0.00
6-9m	SUM82	Q	5	0.000	0.000	0.00	0.000	0.00

Appendix A, Continued

Species=*LAMINARIA DIGITATA*

Depth range	Sample period	T	N	Arithmetic Mean	Mean of log transformed data	Standard error (log_{10})	Geometric Mean	Percent of biomass
0-2m	SUM79	C	5	2.200	0.220	0.22	0.700	0.10
0-2m	SUM79	E	5	19.100	0.400	0.40	1.500	0.80
0-2m	SPR80	C	5	1.000	0.180	0.14	0.500	0.00
0-2m	AUT80	C	4	9.800	0.400	0.40	1.500	0.30
0-2m	AUT80	E	5	0.100	0.030	0.03	0.100	0.00
0-2m	SPR81	E	3	680.700	2.000	1.00	99.000	18.50
0-2m	SUM81	C	5	0.000	0.000	0.00	0.000	0.00
0-2m	SUM81	E	5	0.000	0.000	0.00	0.000	0.00
0-2m	SUM82	C	10	28.100	0.580	0.27	2.800	0.50
0-2m	SUM82	E	10	0.500	0.080	0.08	0.200	0.00
2-3m	SUM79	C	5	+	.	.	.	0.00
2-3m	SUM79	E	5	0.000	0.000	0.00	0.000	0.00
2-3m	AUT79	C	3	0.000	0.000	0.00	0.000	0.00
2-3m	SPR80	C	5	0.000	0.000	0.00	0.000	0.00
2-3m	AUT80	E	5	0.000	0.000	0.00	0.000	0.00
2-3m	SPR81	C	5	0.100	0.040	0.04	0.100	0.10
2-3m	SPR81	E	5	429.400	1.070	0.58	10.700	18.10
2-3m	SUM81	C	5	0.200	0.060	0.06	0.100	0.00
2-3m	SUM81	E	6	357.600	1.110	0.61	11.900	15.00
2-3m	SPR82	C	5	0.000	0.000	0.00	0.000	0.00
2-3m	SPR82	E	6	0.000	0.000	0.00	0.000	0.00
2-3m	SPR82	Q	5	37.300	1.420	0.22	25.300	3.80
2-3m	SUM82	C	10	0.000	0.000	0.00	0.000	0.00
2-3m	SUM82	E	10	1.800	0.160	0.13	0.400	0.10
2-3m	SUM82	Q	5	17.600	0.490	0.37	2.100	0.70
6-9m	SUM79	C	5	0.000	0.000	0.00	0.000	0.00
6-9m	SUM79	E	5	0.000	0.000	0.00	0.000	0.00
6-9m	AUT79	C	4	0.000	0.000	0.00	0.000	0.00
6-9m	SPR80	C	5	0.000	0.000	0.00	0.000	0.00
6-9m	AUT80	C	5	0.000	0.000	0.00	0.000	0.00
6-9m	AUT80	E	5	0.000	0.000	0.00	0.000	0.00
6-9m	SPR81	C	5	0.000	0.000	0.00	0.000	0.00
6-9m	SPR81	E	5	590.600	1.210	0.74	15.200	49.70
6-9m	SUM81	C	5	0.000	0.000	0.00	0.000	0.00
6-9m	SUM81	E	5	27.200	0.860	0.40	6.200	2.80
6-9m	SPR82	C	5	0.000	0.000	0.00	0.000	0.00
6-9m	SPR82	E	5	646.800	0.700	0.70	4.000	48.60
6-9m	SUM82	C	10	+	.	.	.	0.00
6-9m	SUM82	E	10	135.600	0.620	0.36	3.200	5.70
6-9m	SUM82	Q	5	+	.	.	.	0.00

Appendix A, Continued

Species=*MONOSTROMA GREVILLEI*

Depth range	Sample period	T	N	Arithmetic Mean	Mean of log transformed data	Standard error (log_{10})	Geometric Mean	Percent of biomass
0-2m	SUM79	C	5	0.000	0.000	0.00	0.000	0.00
0-2m	SUM79	E	5	0.000	0.000	0.00	0.000	0.00
0-2m	SPR80	C	5	0.000	0.000	0.00	0.000	0.00
0-2m	AUT80	C	4	0.000	0.000	0.00	0.000	0.00
0-2m	AUT80	E	5	0.000	0.000	0.00	0.000	0.00
0-2m	SPR81	E	3	0.000	0.000	0.00	0.000	0.00
0-2m	SUM81	C	5	0.000	0.000	0.00	0.000	0.00
0-2m	SUM81	E	5	0.000	0.000	0.00	0.000	0.00
0-2m	SUM82	C	10	0.000	0.000	0.00	0.000	0.00
0-2m	SUM82	E	10	0.000	0.000	0.00	0.000	0.00
2-3m	SUM79	C	5	0.000	0.000	0.00	0.000	0.00
2-3m	SUM79	E	5	0.000	0.000	0.00	0.000	0.00
2-3m	AUT79	C	3	0.000	0.000	0.00	0.000	0.00
2-3m	SPR80	C	5	0.000	0.000	0.00	0.000	0.00
2-3m	AUT80	E	5	0.000	0.000	0.00	0.000	0.00
2-3m	SPR81	C	5	0.000	0.000	0.00	0.000	0.00
2-3m	SPR81	E	5	12.300	1.000	0.16	9.000	0.50
2-3m	SUM81	C	5	0.000	0.000	0.00	0.000	0.00
2-3m	SUM81	E	6	0.000	0.000	0.00	0.000	0.00
2-3m	SPR82	C	5	0.000	0.000	0.00	0.000	0.00
2-3m	SPR82	E	6	0.000	0.000	0.00	0.000	0.00
2-3m	SPR82	Q	5	0.500	0.100	0.10	0.300	0.00
2-3m	SUM82	C	10	0.000	0.000	0.00	0.000	0.00
2-3m	SUM82	E	10	0.000	0.000	0.00	0.000	0.00
2-3m	SUM82	Q	5	0.000	0.000	0.00	0.000	0.00
6-9m	SUM79	C	5	0.000	0.000	0.00	0.000	0.00
6-9m	SUM79	E	5	0.000	0.000	0.00	0.000	0.00
6-9m	AUT79	C	4	0.000	0.000	0.00	0.000	0.00
6-9m	SPR80	C	5	0.000	0.000	0.00	0.000	0.00
6-9m	AUT80	C	5	0.000	0.000	0.00	0.000	0.00
6-9m	AUT80	E	5	0.000	0.000	0.00	0.000	0.00
6-9m	SPR81	C	5	0.000	0.000	0.00	0.000	0.00
6-9m	SPR81	E	5	0.000	0.000	0.00	0.000	0.00
6-9m	SUM81	C	5	0.000	0.000	0.00	0.000	0.00
6-9m	SUM81	E	5	0.000	0.000	0.00	0.000	0.00
6-9m	SPR82	C	5	0.000	0.000	0.00	0.000	0.00
6-9m	SPR82	E	5	0.000	0.000	0.00	0.000	0.00
6-9m	SUM82	C	10	0.000	0.000	0.00	0.000	0.00
6-9m	SUM82	E	10	0.000	0.000	0.00	0.000	0.00
6-9m	SUM82	Q	5	0.000	0.000	0.00	0.000	0.00

Appendix A, Continued

Species=*PALMARIA PALMATA*

Depth range	Sample period	T	N	Arithmetic Mean	Mean of log transformed data	Standard error (log_{10})	Geometric Mean	Percent of biomass
0-2m	SUM79	C	5	0.000	+	0.01	0.000	0.00
0-2m	SUM79	E	5	+	.	.	.	0.00
0-2m	SPR80	C	5	0.000	0.000	0.00	0.000	0.00
0-2m	AUT80	C	4	0.500	0.130	0.12	0.300	0.00
0-2m	AUT80	E	5	+	.	.	.	0.00
0-2m	SPR81	E	3	0.000	0.000	0.00	0.000	0.00
0-2m	SUM81	C	5	1.000	0.190	0.15	0.500	0.00
0-2m	SUM81	E	5	0.000	0.000	0.00	0.000	0.00
0-2m	SUM82	C	10	8.300	0.490	0.21	2.100	0.10
0-2m	SUM82	E	10	0.000	0.000	0.00	0.000	0.00
2-3m	SUM79	C	5	0.000	0.000	0.00	0.000	0.00
2-3m	SUM79	E	5	0.000	0.000	0.00	0.000	0.00
2-3m	AUT79	C	3	0.000	0.000	0.00	0.000	0.00
2-3m	SPR80	C	5	0.000	0.000	0.00	0.000	0.00
2-3m	AUT80	E	5	+	.	.	.	0.00
2-3m	SPR81	C	5	0.000	0.000	0.00	0.000	0.00
2-3m	SPR81	E	5	0.000	0.000	0.00	0.000	0.00
2-3m	SUM81	C	5	0.000	0.000	0.00	0.000	0.00
2-3m	SUM81	E	6	0.000	0.000	0.00	0.000	0.00
2-3m	SPR82	C	5	0.000	0.000	0.00	0.000	0.00
2-3m	SPR82	E	6	1.600	0.170	0.17	0.500	0.00
2-3m	SPR82	Q	5	0.000	0.000	0.00	0.000	0.00
2-3m	SUM82	C	10	+	.	.	.	0.00
2-3m	SUM82	E	10	0.100	0.040	0.03	0.100	0.00
2-3m	SUM82	Q	5	0.000	0.000	0.00	0.000	0.00
6-9m	SUM79	C	5	0.000	0.000	0.00	0.000	0.00
6-9m	SUM79	E	5	0.000	0.000	0.00	0.000	0.00
6-9m	AUT79	C	4	0.000	0.000	0.00	0.000	0.00
6-9m	SPR80	C	5	0.000	0.000	0.00	0.000	0.00
6-9m	AUT80	C	5	0.000	0.000	0.00	0.000	0.00
6-9m	AUT80	E	5	0.000	0.000	0.00	0.000	0.00
6-9m	SPR81	C	5	0.000	0.000	0.00	0.000	0.00
6-9m	SPR81	E	5	0.000	0.000	0.00	0.000	0.00
6-9m	SUM81	C	5	0.000	0.000	0.00	0.000	0.00
6-9m	SUM81	E	5	0.000	0.000	0.00	0.000	0.00
6-9m	SPR82	C	5	0.000	0.000	0.00	0.000	0.00
6-9m	SPR82	E	5	0.000	0.000	0.00	0.000	0.00
6-9m	SUM82	C	10	0.000	0.000	0.00	0.000	0.00
6-9m	SUM82	E	10	0.000	0.000	0.00	0.000	0.00
6-9m	SUM82	Q	5	0.000	0.000	0.00	0.000	0.00

Appendix A, Continued

Species=*PETALONIA FASCIA*

Depth range	Sample period	T	N	Arithmetic Mean	Mean of log transformed	Standard error	Geometric Mean	Percent of biomass
0-2m	SUM79	C	5	3.500	0.510	0.18	2.200	0.10
0-2m	SUM79	E	5	20.000	1.230	0.16	16.000	0.90
0-2m	SPR80	C	5	13.400	0.640	0.32	3.400	0.40
0-2m	AUT80	C	4	0.200	0.060	0.06	0.100	0.00
0-2m	AUT80	E	5	48.500	1.140	0.39	12.800	2.10
0-2m	SPR81	E	3	0.000	0.000	0.00	0.000	0.00
0-2m	SUM81	C	5	0.000	0.000	0.00	0.000	0.00
0-2m	SUM81	E	5	0.200	0.060	0.04	0.100	0.00
0-2m	SUM82	C	10	2.000	0.170	0.13	0.500	0.00
0-2m	SUM82	E	10	0.000	0.000	0.00	0.000	0.00
2-3m	SUM79	C	5	0.000	0.000	0.00	0.000	0.00
2-3m	SUM79	E	5	0.000	0.000	0.00	0.000	0.00
2-3m	AUT79	C	3	0.000	0.000	0.00	0.000	0.00
2-3m	SPR80	C	5	0.000	0.000	0.00	0.000	0.00
2-3m	AUT80	E	5	0.000	0.000	0.00	0.000	0.00
2-3m	SPR81	C	5	0.000	+	0.01	0.000	0.00
2-3m	SPR81	E	5	1.900	0.330	0.16	1.100	0.10
2-3m	SUM81	C	5	0.600	0.160	0.10	0.400	0.10
2-3m	SUM81	E	6	0.100	0.030	0.03	0.100	0.00
2-3m	SPR82	C	5	0.000	0.000	0.00	0.000	0.00
2-3m	SPR82	E	6	0.000	0.000	0.00	0.000	0.00
2-3m	SPR82	Q	5	0.300	0.070	0.07	0.200	0.00
2-3m	SUM82	C	10	1.600	0.370	0.07	1.300	0.20
2-3m	SUM82	E	10	0.000	0.000	0.00	0.000	0.00
2-3m	SUM82	Q	5	0.300	0.070	0.07	0.200	0.00
6-9m	SUM79	C	5	0.000	0.000	0.00	0.000	0.00
6-9m	SUM79	E	5	0.000	0.000	0.00	0.000	0.00
6-9m	AUT79	C	4	0.000	0.000	0.00	0.000	0.00
6-9m	SPR80	C	5	0.000	0.000	0.00	0.000	0.00
6-9m	AUT80	C	5	0.000	0.000	0.00	0.000	0.00
6-9m	AUT80	E	5	+	.	.	.	0.00
6-9m	SPR81	C	5	0.000	0.000	0.00	0.000	0.00
6-9m	SPR81	E	5	0.000	+	0.01	0.000	0.00
6-9m	SUM81	C	5	0.000	0.000	0.00	0.000	0.00
6-9m	SUM81	E	5	2.800	0.440	0.17	1.800	0.30
6-9m	SPR82	C	5	0.000	0.000	0.00	0.000	0.00
6-9m	SPR82	E	5	0.000	0.000	0.00	0.000	0.00
6-9m	SUM82	C	10	2.400	0.260	0.13	0.800	0.40
6-9m	SUM82	E	10	0.000	0.000	0.00	0.000	0.00
6-9m	SUM82	Q	5	1.000	0.250	0.11	0.800	0.10

Appendix A, Continued

Species=*PETALONIA ZOSTERIFOLIA*

Depth range	Sample period	T	N	Arithmetic Mean	Mean of log transformed data	Standard error (log_{10})	Geometric Mean	Percent of biomass
0-2m	SUM79	C	5	0.000	0.000	0.00	0.000	0.00
0-2m	SUM79	E	5	0.200	0.080	0.04	0.200	0.00
0-2m	SPR80	C	5	0.000	0.000	0.00	0.000	0.00
0-2m	AUT80	C	4	0.000	0.000	0.00	0.000	0.00
0-2m	AUT80	E	5	0.300	0.100	0.06	0.300	0.00
0-2m	SPR81	E	3	0.000	0.000	0.00	0.000	0.00
0-2m	SUM81	C	5	0.000	0.000	0.00	0.000	0.00
0-2m	SUM81	E	5	0.000	0.000	0.00	0.000	0.00
0-2m	SUM82	C	10	0.000	0.000	0.00	0.000	0.00
0-2m	SUM82	E	10	0.000	0.000	0.00	0.000	0.00
2-3m	SUM79	C	5	0.000	0.000	0.00	0.000	0.00
2-3m	SUM79	E	5	0.000	0.000	0.00	0.000	0.00
2-3m	AUT79	C	3	0.000	0.000	0.00	0.000	0.00
2-3m	SPR80	C	5	0.000	0.000	0.00	0.000	0.00
2-3m	AUT80	E	5	0.000	0.000	0.00	0.000	0.00
2-3m	SPR81	C	5	0.000	0.000	0.00	0.000	0.00
2-3m	SPR81	E	5	0.000	0.000	0.00	0.000	0.00
2-3m	SUM81	C	5	0.000	0.000	0.00	0.000	0.00
2-3m	SUM81	E	6	0.000	0.000	0.00	0.000	0.00
2-3m	SPR82	C	5	0.000	0.000	0.00	0.000	0.00
2-3m	SPR82	E	6	0.000	0.000	0.00	0.000	0.00
2-3m	SPR82	Q	5	0.000	0.000	0.00	0.000	0.00
2-3m	SUM82	C	10	0.000	0.000	0.00	0.000	0.00
2-3m	SUM82	E	10	0.000	0.000	0.00	0.000	0.00
2-3m	SUM82	Q	5	0.000	0.000	0.00	0.000	0.00
6-9m	SUM79	C	5	0.000	0.000	0.00	0.000	0.00
6-9m	SUM79	E	5	0.000	0.000	0.00	0.000	0.00
6-9m	AUT79	C	4	0.000	0.000	0.00	0.000	0.00
6-9m	SPR80	C	5	0.000	0.000	0.00	0.000	0.00
6-9m	AUT80	C	5	0.000	0.000	0.00	0.000	0.00
6-9m	AUT80	E	5	0.000	0.000	0.00	0.000	0.00
6-9m	SPR81	C	5	0.000	0.000	0.00	0.000	0.00
6-9m	SPR81	E	5	0.000	0.000	0.00	0.000	0.00
6-9m	SUM81	C	5	0.000	0.000	0.00	0.000	0.00
6-9m	SUM81	E	5	+	.	.	.	0.00
6-9m	SPR82	C	5	0.000	0.000	0.00	0.000	0.00
6-9m	SPR82	E	5	0.000	0.000	0.00	0.000	0.00
6-9m	SUM82	C	10	0.000	0.000	0.00	0.000	0.00
6-9m	SUM82	E	10	0.000	0.000	0.00	0.000	0.00
6-9m	SUM82	Q	5	0.000	0.000	0.00	0.000	0.00

Appendix A, Continued

Species=*PHYCODRYS RUBENS*

Depth range	Sample period	T	N	Arithmetic Mean	Mean of log transformed data	Standard error (log_{10})	Geometric Mean	Percent of biomass
0-2m	SUM79	C	5	0.000	0.000	0.00	0.000	0.00
0-2m	SUM79	E	5	0.000	0.000	0.00	0.000	0.00
0-2m	SPR80	C	5	0.000	0.000	0.00	0.000	0.00
0-2m	AUT80	C	4	0.000	0.000	0.00	0.000	0.00
0-2m	AUT80	E	5	0.000	0.000	0.00	0.000	0.00
0-2m	SPR81	E	3	0.100	0.030	0.03	0.100	0.00
0-2m	SUM81	C	5	0.000	0.000	0.00	0.000	0.00
0-2m	SUM81	E	5	0.000	0.000	0.00	0.000	0.00
0-2m	SUM82	C	10	0.000	0.000	0.00	0.000	0.00
0-2m	SUM82	E	10	0.000	0.000	0.00	0.000	0.00
2-3m	SUM79	C	5	0.000	0.000	0.00	0.000	0.00
2-3m	SUM79	E	5	0.000	0.000	0.00	0.000	0.00
2-3m	AUT79	C	3	0.000	0.000	0.00	0.000	0.00
2-3m	SPR80	C	5	0.000	0.000	0.00	0.000	0.00
2-3m	AUT80	E	5	0.000	0.000	0.00	0.000	0.00
2-3m	SPR81	C	5	0.000	0.000	0.00	0.000	0.00
2-3m	SPR81	E	5	0.000	0.000	0.00	0.000	0.00
2-3m	SUM81	C	5	0.000	0.000	0.00	0.000	0.00
2-3m	SUM81	E	6	0.000	0.000	0.00	0.000	0.00
2-3m	SPR82	C	5	0.000	0.000	0.00	0.000	0.00
2-3m	SPR82	E	6	0.000	0.000	0.00	0.000	0.00
2-3m	SPR82	Q	5	0.000	0.000	0.00	0.000	0.00
2-3m	SUM82	C	10	0.000	0.000	0.00	0.000	0.00
2-3m	SUM82	E	10	0.000	0.000	0.00	0.000	0.00
2-3m	SUM82	Q	5	0.000	0.000	0.00	0.000	0.00
6-9m	SUM79	C	5	0.000	0.000	0.00	0.000	0.00
6-9m	SUM79	E	5	0.000	0.000	0.00	0.000	0.00
6-9m	AUT79	C	4	0.000	0.000	0.00	0.000	0.00
6-9m	SPR80	C	5	0.000	0.000	0.00	0.000	0.00
6-9m	AUT80	C	5	0.000	0.000	0.00	0.000	0.00
6-9m	AUT80	E	5	0.000	0.000	0.00	0.000	0.00
6-9m	SPR81	C	5	0.000	0.000	0.00	0.000	0.00
6-9m	SPR81	E	5	0.000	0.000	0.00	0.000	0.00
6-9m	SUM81	C	5	0.000	0.000	0.00	0.000	0.00
6-9m	SUM81	E	5	+	.	.	.	0.00
6-9m	SPR82	C	5	0.000	0.000	0.00	0.000	0.00
6-9m	SPR82	E	5	0.000	0.000	0.00	0.000	0.00
6-9m	SUM82	C	10	0.000	0.000	0.00	0.000	0.00
6-9m	SUM82	E	10	+	.	.	.	0.00
6-9m	SUM82	Q	5	0.000	0.000	0.00	0.000	0.00

Appendix A, Continued

Species=*PILAYELLA LITTORALIS*

Depth range	Sample period	T	N	Arithmetic Mean	Mean of log transformed data	Standard error (log_{10})	Geometric Mean	Percent of biomass
0-2m	SUM79	C	5	0.900	0.230	0.10	0.700	0.00
0-2m	SUM79	E	5	0.600	0.200	0.06	0.600	0.00
0-2m	SPR80	C	5	11.700	0.720	0.28	4.200	0.40
0-2m	AUT80	C	4	0.000	0.000	0.00	0.000	0.00
0-2m	AUT80	E	5	1.900	0.200	0.20	0.600	0.10
0-2m	SPR81	E	3	0.400	0.140	0.04	0.400	0.00
0-2m	SUM81	C	5	0.000	0.000	0.00	0.000	0.00
0-2m	SUM81	E	5	0.400	0.090	0.09	0.200	0.00
0-2m	SUM82	C	10	+	.	.	.	0.00
0-2m	SUM82	E	10	+	.	.	.	0.00
2-3m	SUM79	C	5	0.100	0.030	0.03	0.100	0.50
2-3m	SUM79	E	5	+	.	.	.	0.00
2-3m	AUT79	C	3	0.000	0.000	0.00	0.000	0.00
2-3m	SPR80	C	5	0.000	0.000	0.00	0.000	0.00
2-3m	AUT80	E	5	0.000	0.000	0.00	0.000	0.00
2-3m	SPR81	C	5	0.800	0.140	0.13	0.400	0.60
2-3m	SPR81	E	5	17.100	1.090	0.19	11.300	0.70
2-3m	SUM81	C	5	0.000	0.000	0.00	0.000	0.00
2-3m	SUM81	E	6	0.000	0.000	0.00	0.000	0.00
2-3m	SPR82	C	5	0.000	0.000	0.00	0.000	0.00
2-3m	SPR82	E	6	+	.	.	.	0.00
2-3m	SPR82	Q	5	+	.	.	.	0.00
2-3m	SUM82	C	10	+	.	.	.	0.00
2-3m	SUM82	E	10	0.000	0.000	0.00	0.000	0.00
2-3m	SUM82	Q	5	0.000	0.000	0.00	0.000	0.00
6-9m	SUM79	C	5	0.000	+	0.01	0.000	0.10
6-9m	SUM79	E	5	+	.	.	.	0.00
6-9m	AUT79	C	4	0.000	0.000	0.00	0.000	0.00
6-9m	SPR80	C	5	0.000	0.000	0.00	0.000	0.00
6-9m	AUT80	C	5	0.000	0.000	0.00	0.000	0.00
6-9m	AUT80	E	5	0.000	0.000	0.00	0.000	0.00
6-9m	SPR81	C	5	0.000	0.000	0.00	0.000	0.00
6-9m	SPR81	E	5	0.600	0.140	0.10	0.400	0.00
6-9m	SUM81	C	5	0.000	0.000	0.00	0.000	0.00
6-9m	SUM81	E	5	0.000	0.000	0.00	0.000	0.00
6-9m	SPR82	C	5	0.000	0.000	0.00	0.000	0.00
6-9m	SPR82	E	5	0.000	0.000	0.00	0.000	0.00
6-9m	SUM82	C	10	0.000	0.000	0.00	0.000	0.00
6-9m	SUM82	E	10	0.000	0.000	0.00	0.000	0.00
6-9m	SUM82	Q	5	+	.	.	.	0.00

Appendix A, Continued

Species=*POLYSIPHONIA FLEXICAULIS*

Depth range	Sample period	T	N	Arithmetic Mean	Mean of log transformed data	Standard error (log_{10})	Geometric Mean	Percent of biomass
0-2m	SUM79	C	5	+	.	.	.	0.00
0-2m	SUM79	E	5	0.200	0.060	0.05	0.100	0.00
0-2m	SPR80	C	5	1.300	0.210	0.17	0.600	0.00
0-2m	AUT80	C	4	0.000	0.000	0.00	0.000	0.00
0-2m	AUT80	E	5	0.200	0.060	0.05	0.100	0.00
0-2m	SPR81	E	3	1.600	0.330	0.20	1.100	0.00
0-2m	SUM81	C	5	0.000	0.000	0.00	0.000	0.00
0-2m	SUM81	E	5	0.000	0.000	0.00	0.000	0.00
0-2m	SUM82	C	10	+	.	.	.	0.00
0-2m	SUM82	E	10	+	.	.	.	0.00
2-3m	SUM79	C	5	0.200	0.060	0.06	0.100	1.20
2-3m	SUM79	E	5	0.000	0.000	0.00	0.000	0.00
2-3m	AUT79	C	3	0.000	0.000	0.00	0.000	0.00
2-3m	SPR80	C	5	0.000	0.000	0.00	0.000	0.00
2-3m	AUT80	E	5	18.800	0.820	0.35	5.600	57.30
2-3m	SPR81	C	5	0.000	0.000	0.00	0.000	0.00
2-3m	SPR81	E	5	0.700	0.220	0.07	0.700	0.00
2-3m	SUM81	C	5	0.000	0.000	0.00	0.000	0.00
2-3m	SUM81	E	6	10.700	0.440	0.29	1.800	0.40
2-3m	SPR82	C	5	0.000	0.000	0.00	0.000	0.00
2-3m	SPR82	E	6	0.000	0.000	0.00	0.000	0.00
2-3m	SPR82	Q	5	0.000	0.000	0.00	0.000	0.00
2-3m	SUM82	C	10	0.000	+	0.01	0.000	0.00
2-3m	SUM82	E	10	0.000	0.000	0.00	0.000	0.00
2-3m	SUM82	Q	5	1.500	0.300	0.14	1.000	0.10
6-9m	SUM79	C	5	0.000	0.000	0.00	0.000	0.00
6-9m	SUM79	E	5	0.000	0.000	0.00	0.000	0.00
6-9m	AUT79	C	4	0.100	0.040	0.04	0.100	81.60
6-9m	SPR80	C	5	0.000	0.000	0.00	0.000	0.00
6-9m	AUT80	C	5	0.000	0.000	0.00	0.000	0.00
6-9m	AUT80	E	5	3.200	0.470	0.18	2.000	13.40
6-9m	SPR81	C	5	0.000	0.000	0.00	0.000	0.00
6-9m	SPR81	E	5	4.000	0.350	0.24	1.200	0.30
6-9m	SUM81	C	5	0.000	0.000	0.00	0.000	0.00
6-9m	SUM81	E	5	31.900	0.630	0.43	3.300	3.20
6-9m	SPR82	C	5	0.000	0.000	0.00	0.000	0.00
6-9m	SPR82	E	5	1.900	0.230	0.19	0.700	0.10
6-9m	SUM82	C	10	0.000	0.000	0.00	0.000	0.00
6-9m	SUM82	E	10	87.300	1.320	0.29	19.900	3.70
6-9m	SUM82	Q	5	0.200	0.060	0.06	0.100	0.00

Appendix A, Continued

Species=*POLYSIPHONIA URCEOLATA*

Depth range	Sample period	T	N	Arithmetic Mean	Mean of log transformed data	Standard error (log_{10})	Geometric Mean	Percent of biomass
0-2m	SUM79	C	5	14.400	0.990	0.24	8.800	0.60
0-2m	SUM79	E	5	8.900	0.830	0.19	5.800	0.40
0-2m	SPR80	C	5	17.600	0.840	0.34	5.900	0.60
0-2m	AUT80	C	4	6.700	0.510	0.31	2.200	0.20
0-2m	AUT80	E	5	19.300	0.750	0.36	4.600	0.80
0-2m	SPR81	E	3	71.500	1.620	0.33	40.700	1.90
0-2m	SUM81	C	5	2.700	0.230	0.23	0.700	0.00
0-2m	SUM81	E	5	88.500	0.880	0.47	6.600	1.60
0-2m	SUM82	C	10	25.800	0.770	0.25	4.900	0.40
0-2m	SUM82	E	10	2.300	0.310	0.13	1.000	0.00
2-3m	SUM79	C	5	2.600	0.240	0.23	0.700	15.10
2-3m	SUM79	E	5	0.000	+	0.01	0.000	2.70
2-3m	AUT79	C	3	+	.	.	.	0.00
2-3m	SPR80	C	5	+	.	.	.	0.00
2-3m	AUT80	E	5	5.200	0.590	0.21	2.900	15.90
2-3m	SPR81	C	5	1.000	0.200	0.13	0.600	0.70
2-3m	SPR81	E	5	34.600	1.450	0.14	27.200	1.50
2-3m	SUM81	C	5	0.500	0.150	0.06	0.400	0.10
2-3m	SUM81	E	6	22.300	1.260	0.16	17.200	0.90
2-3m	SPR82	C	5	+	.	.	.	0.00
2-3m	SPR82	E	6	0.100	0.020	0.02	0.000	0.00
2-3m	SPR82	Q	5	9.600	0.380	0.33	1.400	1.00
2-3m	SUM82	C	10	1.500	0.290	0.10	0.900	0.20
2-3m	SUM82	E	10	0.600	0.120	0.07	0.300	0.00
2-3m	SUM82	Q	5	+	.	.	.	0.00
6-9m	SUM79	C	5	0.400	0.100	0.09	0.300	1.70
6-9m	SUM79	E	5	+	.	.	.	0.00
6-9m	AUT79	C	4	+	.	.	.	0.00
6-9m	SPR80	C	5	+	.	.	.	0.00
6-9m	AUT80	C	5	+	.	.	.	0.00
6-9m	AUT80	E	5	15.300	1.010	0.24	9.200	65.30
6-9m	SPR81	C	5	0.100	0.020	0.01	0.000	50.00
6-9m	SPR81	E	5	4.900	0.300	0.28	1.000	0.40
6-9m	SUM81	C	5	+	.	.	.	0.00
6-9m	SUM81	E	5	49.800	1.050	0.45	10.200	5.10
6-9m	SPR82	C	5	+	.	.	.	0.00
6-9m	SPR82	E	5	0.300	0.070	0.07	0.200	0.00
6-9m	SUM82	C	10	1.400	0.180	0.11	0.500	0.30
6-9m	SUM82	E	10	11.900	0.440	0.22	1.800	0.50
6-9m	SUM82	Q	5	1.500	0.230	0.17	0.700	0.20

Appendix A, Continued

Species=*PORPHYRA SPP.*

Depth range	Sample period	T	N	Arithmetic Mean	Mean of log transformed data	Standard error (log_{10})	Geometric Mean	Percent of biomass
0-2m	SUM79	C	5	0.200	0.060	0.05	0.100	0.00
0-2m	SUM79	E	5	+	.	.	.	0.00
0-2m	SPR80	C	5	+	.	.	.	0.00
0-2m	AUT80	C	4	0.000	0.000	0.00	0.000	0.00
0-2m	AUT80	E	5	0.000	0.000	0.00	0.000	0.00
0-2m	SPR81	E	3	0.000	0.000	0.00	0.000	0.00
0-2m	SUM81	C	5	0.000	0.000	0.00	0.000	0.00
0-2m	SUM81	E	5	0.000	0.000	0.00	0.000	0.00
0-2m	SUM82	C	10	0.000	0.000	0.00	0.000	0.00
0-2m	SUM82	E	10	0.000	0.000	0.00	0.000	0.00
2-3m	SUM79	C	5	0.000	0.000	0.00	0.000	0.00
2-3m	SUM79	E	5	0.000	0.000	0.00	0.000	0.00
2-3m	AUT79	C	3	0.000	0.000	0.00	0.000	0.00
2-3m	SPR80	C	5	0.000	0.000	0.00	0.000	0.00
2-3m	AUT80	E	5	0.000	0.000	0.00	0.000	0.00
2-3m	SPR81	C	5	0.000	0.020	0.01	0.000	0.00
2-3m	SPR81	E	5	0.000	0.020	0.01	0.000	0.00
2-3m	SUM81	C	5	0.000	0.000	0.00	0.000	0.00
2-3m	SUM81	E	6	+	.	.	.	0.00
2-3m	SPR82	C	5	0.000	0.000	0.00	0.000	0.00
2-3m	SPR82	E	6	0.000	0.000	0.00	0.000	0.00
2-3m	SPR82	Q	5	0.000	0.000	0.00	0.000	0.00
2-3m	SUM82	C	10	+	.	.	.	0.00
2-3m	SUM82	E	10	+	.	.	.	0.00
2-3m	SUM82	Q	5	0.000	0.000	0.00	0.000	0.00
6-9m	SUM79	C	5	+	.	.	.	0.00
6-9m	SUM79	E	5	0.000	0.000	0.00	0.000	0.00
6-9m	AUT79	C	4	0.000	0.000	0.00	0.000	0.00
6-9m	SPR80	C	5	0.000	0.000	0.00	0.000	0.00
6-9m	AUT80	C	5	0.000	0.000	0.00	0.000	0.00
6-9m	AUT80	E	5	+	.	.	.	0.00
6-9m	SPR81	C	5	0.000	0.000	0.00	0.000	0.00
6-9m	SPR81	E	5	0.000	+	0.01	0.000	0.00
6-9m	SUM81	C	5	0.000	0.000	0.00	0.000	0.00
6-9m	SUM81	E	5	0.000	+	0.01	0.000	0.00
6-9m	SPR82	C	5	0.000	0.000	0.00	0.000	0.00
6-9m	SPR82	E	5	0.000	0.000	0.00	0.000	0.00
6-9m	SUM82	C	10	0.100	0.020	0.02	0.000	0.00
6-9m	SUM82	E	10	+	.	.	.	0.00
6-9m	SUM82	Q	5	0.000	0.000	0.00	0.000	0.00

Appendix A, Continued

Species=*PTILOTA SERRATA*

Depth range	Sample period	T	N	Arithmetic Mean	Mean of log transformed	Standard error	Geometric Mean	Percent of biomass
0-2m	SUM79	C	5	+	.	.	.	0.00
0-2m	SUM79	E	5	+	.	.	.	0.00
0-2m	SPR80	C	5	0.000	0.000	0.00	0.000	0.00
0-2m	AUT80	C	4	0.000	0.000	0.00	0.000	0.00
0-2m	AUT80	E	5	0.000	0.000	0.00	0.000	0.00
0-2m	SPR81	E	3	0.000	0.000	0.00	0.000	0.00
0-2m	SUM81	C	5	0.000	0.000	0.00	0.000	0.00
0-2m	SUM81	E	5	0.000	0.000	0.00	0.000	0.00
0-2m	SUM82	C	10	+	.	.	.	0.00
0-2m	SUM82	E	10	0.000	0.000	0.00	0.000	0.00
2-3m	SUM79	C	5	+	.	.	.	0.00
2-3m	SUM79	E	5	+	.	.	.	0.00
2-3m	AUT79	C	3	+	.	.	.	0.00
2-3m	SPR80	C	5	+	.	.	.	0.00
2-3m	AUT80	E	5	+	.	.	.	0.00
2-3m	SPR81	C	5	0.000	+	0.01	0.000	0.00
2-3m	SPR81	E	5	0.000	+	0.01	0.000	0.00
2-3m	SUM81	C	5	+	.	.	.	0.00
2-3m	SUM81	E	6	+	.	.	.	0.00
2-3m	SPR82	C	5	0.000	0.000	0.00	0.000	0.00
2-3m	SPR82	E	6	0.000	0.000	0.00	0.000	0.00
2-3m	SPR82	Q	5	0.000	0.000	0.00	0.000	0.00
2-3m	SUM82	C	10	+	.	.	.	0.00
2-3m	SUM82	E	10	0.000	0.000	0.00	0.000	0.00
2-3m	SUM82	Q	5	0.000	0.000	0.00	0.000	0.00
6-9m	SUM79	C	5	+	.	.	.	0.00
6-9m	SUM79	E	5	0.100	0.040	0.02	0.100	82.30
6-9m	AUT79	C	4	+	.	.	.	0.00
6-9m	SPR80	C	5	+	.	.	.	0.00
6-9m	AUT80	C	5	+	.	.	.	0.00
6-9m	AUT80	E	5	+	.	.	.	0.00
6-9m	SPR81	C	5	0.000	0.020	0.01	0.000	33.30
6-9m	SPR81	E	5	3.000	0.310	0.23	1.000	0.30
6-9m	SUM81	C	5	0.000	0.000	0.00	0.000	0.00
6-9m	SUM81	E	5	0.800	0.170	0.13	0.500	0.10
6-9m	SPR82	C	5	+	.	.	.	0.00
6-9m	SPR82	E	5	0.200	0.050	0.05	0.100	0.00
6-9m	SUM82	C	10	+	.	.	.	0.00
6-9m	SUM82	E	10	3.400	0.400	0.15	1.500	0.10
6-9m	SUM82	Q	5	0.000	0.000	0.00	0.000	0.00

Appendix A, Continued

Species=*PUNCTARIA PLANTAGINEA*

Depth range	Sample period	T	N	Arithmetic Mean	Mean of log transformed data	Standard error (log_{10})	Geometric Mean	Percent of biomass
0-2m	SUM79	C	5	0.000	0.000	0.00	0.000	0.00
0-2m	SUM79	E	5	3.900	0.600	0.16	3.000	0.20
0-2m	SPR80	C	5	0.000	0.000	0.00	0.000	0.00
0-2m	AUT80	C	4	0.000	0.000	0.00	0.000	0.00
0-2m	AUT80	E	5	1.600	0.190	0.19	0.500	0.10
0-2m	SPR81	E	3	0.000	0.000	0.00	0.000	0.00
0-2m	SUM81	C	5	0.000	0.000	0.00	0.000	0.00
0-2m	SUM81	E	5	0.000	0.000	0.00	0.000	0.00
0-2m	SUM82	C	10	0.000	0.000	0.00	0.000	0.00
0-2m	SUM82	E	10	0.000	0.000	0.00	0.000	0.00
2-3m	SUM79	C	5	0.000	0.000	0.00	0.000	0.00
2-3m	SUM79	E	5	0.000	0.000	0.00	0.000	0.00
2-3m	AUT79	C	3	0.000	0.000	0.00	0.000	0.00
2-3m	SPR80	C	5	0.000	0.000	0.00	0.000	0.00
2-3m	AUT80	E	5	0.000	0.000	0.00	0.000	0.00
2-3m	SPR81	C	5	0.000	0.000	0.00	0.000	0.00
2-3m	SPR81	E	5	0.000	0.000	0.00	0.000	0.00
2-3m	SUM81	C	5	0.000	0.000	0.00	0.000	0.00
2-3m	SUM81	E	6	0.000	0.000	0.00	0.000	0.00
2-3m	SPR82	C	5	0.000	0.000	0.00	0.000	0.00
2-3m	SPR82	E	6	0.000	0.000	0.00	0.000	0.00
2-3m	SPR82	Q	5	0.000	0.000	0.00	0.000	0.00
2-3m	SUM82	C	10	0.000	0.000	0.00	0.000	0.00
2-3m	SUM82	E	10	0.000	0.000	0.00	0.000	0.00
2-3m	SUM82	Q	5	0.000	0.000	0.00	0.000	0.00
6-9m	SUM79	C	5	0.000	0.000	0.00	0.000	0.00
6-9m	SUM79	E	5	0.000	0.000	0.00	0.000	0.00
6-9m	AUT79	C	4	0.000	0.000	0.00	0.000	0.00
6-9m	SPR80	C	5	0.000	0.000	0.00	0.000	0.00
6-9m	AUT80	C	5	0.000	0.000	0.00	0.000	0.00
6-9m	AUT80	E	5	0.000	0.000	0.00	0.000	0.00
6-9m	SPR81	C	5	0.000	0.000	0.00	0.000	0.00
6-9m	SPR81	E	5	0.000	0.000	0.00	0.000	0.00
6-9m	SUM81	C	5	0.000	0.000	0.00	0.000	0.00
6-9m	SUM81	E	5	0.000	0.000	0.00	0.000	0.00
6-9m	SPR82	C	5	0.000	0.000	0.00	0.000	0.00
6-9m	SPR82	E	5	0.000	0.000	0.00	0.000	0.00
6-9m	SUM82	C	10	0.000	0.000	0.00	0.000	0.00
6-9m	SUM82	E	10	0.000	0.000	0.00	0.000	0.00
6-9m	SUM82	Q	5	0.000	0.000	0.00	0.000	0.00

Appendix A, Continued

Species=*RHODOMELA CONFERVOIDES*

Depth range	Sample period	T	N	Arithmetic Mean	Mean of log transformed data	Standard error (log_{10})	Geometric Mean	Percent of biomass
0-2m	SUM79	C	5	0.000	0.000	0.00	0.000	0.00
0-2m	SUM79	E	5	0.500	0.100	0.10	0.300	0.00
0-2m	SPR80	C	5	0.000	0.000	0.00	0.000	0.00
0-2m	AUT80	C	4	0.000	0.000	0.00	0.000	0.00
0-2m	AUT80	E	5	0.000	0.020	0.02	0.000	0.00
0-2m	SPR81	E	3	3.800	0.360	0.36	1.300	0.10
0-2m	SUM81	C	5	0.000	0.000	0.00	0.000	0.00
0-2m	SUM81	E	5	0.000	0.000	0.00	0.000	0.00
0-2m	SUM82	C	10	+	.	.	.	0.00
0-2m	SUM82	E	10	1.000	0.160	0.11	0.400	0.00
2-3m	SUM79	C	5	0.000	0.000	0.00	0.000	0.00
2-3m	SUM79	E	5	0.000	0.000	0.00	0.000	0.00
2-3m	AUT79	C	3	0.000	0.000	0.00	0.000	0.00
2-3m	SPR80	C	5	0.000	0.000	0.00	0.000	0.00
2-3m	AUT80	E	5	0.100	0.030	0.03	0.100	0.20
2-3m	SPR81	C	5	0.000	0.000	0.00	0.000	0.00
2-3m	SPR81	E	5	0.000	0.000	0.00	0.000	0.00
2-3m	SUM81	C	5	0.000	0.000	0.00	0.000	0.00
2-3m	SUM81	E	6	13.900	0.680	0.32	3.800	0.60
2-3m	SPR82	C	5	0.000	0.000	0.00	0.000	0.00
2-3m	SPR82	E	6	0.000	+	0.01	0.000	0.00
2-3m	SPR82	Q	5	0.000	0.000	0.00	0.000	0.00
2-3m	SUM82	C	10	0.000	+	0.01	0.000	0.00
2-3m	SUM82	E	10	0.200	0.060	0.04	0.100	0.00
2-3m	SUM82	Q	5	+	.	.	.	0.00
6-9m	SUM79	C	5	0.000	0.000	0.00	0.000	0.00
6-9m	SUM79	E	5	0.000	0.000	0.00	0.000	0.00
6-9m	AUT79	C	4	0.000	0.000	0.00	0.000	0.00
6-9m	SPR80	C	5	0.000	0.000	0.00	0.000	0.00
6-9m	AUT80	C	5	0.000	0.000	0.00	0.000	0.00
6-9m	AUT80	E	5	0.400	0.110	0.09	0.300	1.80
6-9m	SPR81	C	5	0.000	0.000	0.00	0.000	0.00
6-9m	SPR81	E	5	62.400	0.510	0.50	2.200	5.30
6-9m	SUM81	C	5	0.000	0.000	0.00	0.000	0.00
6-9m	SUM81	E	5	86.000	0.530	0.53	2.400	8.70
6-9m	SPR82	C	5	0.000	0.000	0.00	0.000	0.00
6-9m	SPR82	E	5	81.400	0.680	0.49	3.800	6.10
6-9m	SUM82	C	10	0.000	0.000	0.00	0.000	0.00
6-9m	SUM82	E	10	11.600	0.520	0.23	2.300	0.50
6-9m	SUM82	Q	5	0.000	0.000	0.00	0.000	0.00

Appendix A, Continued

Species=*SACCORHIZA DERMATODEA*

Depth range	Sample period	T	N	Arithmetic Mean	Mean of log transformed	Standard error	Geometric Mean	Percent of biomass
0-2m	SUM79	C	5	11.400	0.530	0.32	2.400	0.50
0-2m	SUM79	E	5	3.800	0.380	0.25	1.400	0.20
0-2m	SPR80	C	5	122.900	1.860	0.22	71.400	3.90
0-2m	AUT80	C	4	1857.500	3.220	0.12	1658.600	48.30
0-2m	AUT80	E	5	749.800	1.640	0.73	42.700	32.90
0-2m	SPR81	E	3	0.000	0.000	0.00	0.000	0.00
0-2m	SUM81	C	5	0.000	0.000	0.00	0.000	0.00
0-2m	SUM81	E	5	0.000	0.000	0.00	0.000	0.00
0-2m	SUM82	C	10	33.300	0.380	0.27	1.400	0.50
0-2m	SUM82	E	10	0.000	0.000	0.00	0.000	0.00
2-3m	SUM79	C	5	0.000	0.000	0.00	0.000	0.00
2-3m	SUM79	E	5	0.000	0.000	0.00	0.000	0.00
2-3m	AUT79	C	3	0.000	0.000	0.00	0.000	0.00
2-3m	SPR80	C	5	0.000	0.000	0.00	0.000	0.00
2-3m	AUT80	E	5	0.000	0.000	0.00	0.000	0.00
2-3m	SPR81	C	5	0.000	0.000	0.00	0.000	0.00
2-3m	SPR81	E	5	3.800	0.260	0.26	0.800	0.20
2-3m	SUM81	C	5	6.600	0.310	0.31	1.000	1.00
2-3m	SUM81	E	6	0.000	0.000	0.00	0.000	0.00
2-3m	SPR82	C	5	0.000	0.000	0.00	0.000	0.00
2-3m	SPR82	E	6	+	.	.	.	0.00
2-3m	SPR82	Q	5	0.000	0.000	0.00	0.000	0.00
2-3m	SUM82	C	10	2.800	0.220	0.15	0.700	0.40
2-3m	SUM82	E	10	0.200	0.050	0.05	0.100	0.00
2-3m	SUM82	Q	5	0.000	0.000	0.00	0.000	0.00
6-9m	SUM79	C	5	0.000	0.000	0.00	0.000	0.00
6-9m	SUM79	E	5	0.000	0.000	0.00	0.000	0.00
6-9m	AUT79	C	4	0.000	0.000	0.00	0.000	0.00
6-9m	SPR80	C	5	0.000	0.000	0.00	0.000	0.00
6-9m	AUT80	C	5	0.000	0.000	0.00	0.000	0.00
6-9m	AUT80	E	5	0.000	0.000	0.00	0.000	0.00
6-9m	SPR81	C	5	0.000	0.000	0.00	0.000	0.00
6-9m	SPR81	E	5	0.000	0.000	0.00	0.000	0.00
6-9m	SUM81	C	5	0.000	0.000	0.00	0.000	0.00
6-9m	SUM81	E	5	5.100	0.280	0.28	0.900	0.50
6-9m	SPR82	C	5	0.000	0.000	0.00	0.000	0.00
6-9m	SPR82	E	5	0.000	0.000	0.00	0.000	0.00
6-9m	SUM82	C	10	0.000	0.000	0.00	0.000	0.00
6-9m	SUM82	E	10	0.000	0.000	0.00	0.000	0.00
6-9m	SUM82	Q	5	0.000	0.000	0.00	0.000	0.00

Appendix A, Continued

Species=*SCAGELIA* corallina

Depth range	Sample period	T	N	Arithmetic Mean	Mean of log transformed data	Standard error (log_{10})	Geometric Mean	Percent of biomass
0-2m	SUM79	C	5	0.000	+	0.01	0.000	0.00
0-2m	SUM79	E	5	+	.	.	.	0.00
0-2m	SPR80	C	5	0.000	+	0.01	0.000	0.00
0-2m	AUT80	C	4	0.000	0.000	0.00	0.000	0.00
0-2m	AUT80	E	5	+	.	.	.	0.00
0-2m	SPR81	E	3	0.200	0.070	0.07	0.200	0.00
0-2m	SUM81	C	5	0.000	0.000	0.00	0.000	0.00
0-2m	SUM81	E	5	0.000	0.020	0.02	0.000	0.00
0-2m	SUM82	C	10	+	.	.	.	0.00
0-2m	SUM82	E	10	+	.	.	.	0.00
2-3m	SUM79	C	5	+	.	.	.	0.00
2-3m	SUM79	E	5	+	.	.	.	0.00
2-3m	AUT79	C	3	+	.	.	.	0.00
2-3m	SPR80	C	5	+	.	.	.	0.00
2-3m	AUT80	E	5	3.000	0.380	0.20	1.400	9.30
2-3m	SPR81	C	5	0.400	0.130	0.08	0.300	0.30
2-3m	SPR81	E	5	0.300	0.110	0.04	0.300	0.00
2-3m	SUM81	C	5	0.400	0.100	0.10	0.300	0.10
2-3m	SUM81	E	6	0.100	0.020	0.02	0.000	0.00
2-3m	SPR82	C	5	0.000	0.000	0.00	0.000	0.00
2-3m	SPR82	E	6	+	.	.	.	0.00
2-3m	SPR82	Q	5	28.100	1.340	0.16	20.900	2.80
2-3m	SUM82	C	10	0.500	0.110	0.07	0.300	0.10
2-3m	SUM82	E	10	+	.	.	.	0.00
2-3m	SUM82	Q	5	3.600	0.260	0.26	0.800	0.20
6-9m	SUM79	C	5	+	.	.	.	0.00
6-9m	SUM79	E	5	+	.	.	.	0.00
6-9m	AUT79	C	4	+	.	.	.	0.00
6-9m	SPR80	C	5	0.000	0.000	0.00	0.000	0.00
6-9m	AUT80	C	5	+	.	.	.	0.00
6-9m	AUT80	E	5	0.900	0.220	0.11	0.700	3.80
6-9m	SPR81	C	5	0.000	0.000	0.00	0.000	0.00
6-9m	SPR81	E	5	3.600	0.340	0.24	1.200	0.30
6-9m	SUM81	C	5	0.000	0.000	0.00	0.000	0.00
6-9m	SUM81	E	5	+	.	.	.	0.00
6-9m	SPR82	C	5	0.000	0.000	0.00	0.000	0.00
6-9m	SPR82	E	5	34.800	0.450	0.45	1.800	2.60
6-9m	SUM82	C	10	0.100	0.040	0.03	0.100	0.00
6-9m	SUM82	E	10	1.800	0.150	0.12	0.400	0.10
6-9m	SUM82	Q	5	0.100	0.030	0.02	0.100	0.00

Appendix A, Continued

Species=*SCYTOSIPHON LOMENTARIA*

Depth range	Sample period	T	N	Arithmetic Mean	Mean of log transformed data	Standard error (log_{10})	Geometric Mean	Percent of biomass
0-2m	SUM79	C	5	32.800	1.190	0.27	14.500	1.40
0-2m	SUM79	E	5	4.800	0.600	0.18	3.000	0.20
0-2m	SPR80	C	5	46.400	1.200	0.32	14.800	1.50
0-2m	AUT80	C	4	0.000	0.000	0.00	0.000	0.00
0-2m	AUT80	E	5	2.700	0.380	0.20	1.400	0.10
0-2m	SPR81	E	3	0.000	0.000	0.00	0.000	0.00
0-2m	SUM81	C	5	0.000	0.000	0.00	0.000	0.00
0-2m	SUM81	E	5	0.000	0.000	0.00	0.000	0.00
0-2m	SUM82	C	10	0.700	0.140	0.08	0.400	0.00
0-2m	SUM82	E	10	0.000	0.000	0.00	0.000	0.00
2-3m	SUM79	C	5	0.000	0.000	0.00	0.000	0.00
2-3m	SUM79	E	5	0.000	0.000	0.00	0.000	0.00
2-3m	AUT79	C	3	0.000	0.000	0.00	0.000	0.00
2-3m	SPR80	C	5	0.000	0.000	0.00	0.000	0.00
2-3m	AUT80	E	5	0.000	0.000	0.00	0.000	0.00
2-3m	SPR81	C	5	1.100	0.190	0.15	0.500	0.80
2-3m	SPR81	E	5	2.300	0.250	0.21	0.800	0.10
2-3m	SUM81	C	5	0.000	0.000	0.00	0.000	0.00
2-3m	SUM81	E	6	0.000	0.000	0.00	0.000	0.00
2-3m	SPR82	C	5	+	.	.	.	0.00
2-3m	SPR82	E	6	0.000	0.000	0.00	0.000	0.00
2-3m	SPR82	Q	5	0.000	0.000	0.00	0.000	0.00
2-3m	SUM82	C	10	1.200	0.210	0.09	0.600	0.20
2-3m	SUM82	E	10	0.000	0.000	0.00	0.000	0.00
2-3m	SUM82	Q	5	0.000	0.000	0.00	0.000	0.00
6-9m	SUM79	C	5	1.400	0.230	0.16	0.700	5.60
6-9m	SUM79	E	5	0.000	0.000	0.00	0.000	0.00
6-9m	AUT79	C	4	0.000	0.000	0.00	0.000	0.00
6-9m	SPR80	C	5	0.000	0.000	0.00	0.000	0.00
6-9m	AUT80	C	5	0.000	0.000	0.00	0.000	0.00
6-9m	AUT80	E	5	0.000	0.000	0.00	0.000	0.00
6-9m	SPR81	C	5	0.000	0.000	0.00	0.000	0.00
6-9m	SPR81	E	5	0.600	0.180	0.07	0.500	0.10
6-9m	SUM81	C	5	0.000	0.000	0.00	0.000	0.00
6-9m	SUM81	E	5	1.600	0.190	0.19	0.500	0.20
6-9m	SPR82	C	5	0.000	0.000	0.00	0.000	0.00
6-9m	SPR82	E	5	0.000	0.000	0.00	0.000	0.00
6-9m	SUM82	C	10	0.000	0.000	0.00	0.000	0.00
6-9m	SUM82	E	10	+	.	.	.	0.00
6-9m	SUM82	Q	5	0.000	0.000	0.00	0.000	0.00

Appendix A, Continued

Species=*SPONGOMORPHA AERUGINOSA*

Depth range	Sample period	T	N	Arithmetic Mean	Mean of log transformed data	Standard error (log_{10})	Geometric Mean	Percent of biomass
0-2m	SUM79	C	5	11.300	0.780	0.26	5.000	0.50
0-2m	SUM79	E	5	18.200	1.120	0.23	12.200	0.80
0-2m	SPR80	C	5	3.400	0.590	0.10	2.900	0.10
0-2m	AUT80	C	4	0.900	0.160	0.16	0.400	0.00
0-2m	AUT80	E	5	2.600	0.400	0.18	1.500	0.10
0-2m	SPR81	E	3	0.000	0.000	0.00	0.000	0.00
0-2m	SUM81	C	5	0.000	0.000	0.00	0.000	0.00
0-2m	SUM81	E	5	0.000	0.000	0.00	0.000	0.00
0-2m	SUM82	C	10	0.000	0.000	0.00	0.000	0.00
0-2m	SUM82	E	10	0.000	0.000	0.00	0.000	0.00
2-3m	SUM79	C	5	+	.	.	.	0.00
2-3m	SUM79	E	5	0.000	+	0.01	0.000	2.00
2-3m	AUT79	C	3	0.000	0.000	0.00	0.000	0.00
2-3m	SPR80	C	5	+	.	.	.	0.00
2-3m	AUT80	E	5	+	.	.	.	0.00
2-3m	SPR81	C	5	0.000	0.000	0.00	0.000	0.00
2-3m	SPR81	E	5	0.000	0.000	0.00	0.000	0.00
2-3m	SUM81	C	5	+	.	.	.	0.00
2-3m	SUM81	E	6	0.000	0.000	0.00	0.000	0.00
2-3m	SPR82	C	5	0.000	0.000	0.00	0.000	0.00
2-3m	SPR82	E	6	0.000	0.000	0.00	0.000	0.00
2-3m	SPR82	Q	5	0.000	0.000	0.00	0.000	0.00
2-3m	SUM82	C	10	0.300	0.060	0.06	0.100	0.00
2-3m	SUM82	E	10	+	.	.	.	0.00
2-3m	SUM82	Q	5	0.000	0.000	0.00	0.000	0.00
6-9m	SUM79	C	5	+	.	.	.	0.00
6-9m	SUM79	E	5	0.000	0.000	0.00	0.000	0.00
6-9m	AUT79	C	4	0.000	0.000	0.00	0.000	0.00
6-9m	SPR80	C	5	0.000	0.000	0.00	0.000	0.00
6-9m	AUT80	C	5	0.000	0.000	0.00	0.000	0.00
6-9m	AUT80	E	5	+	.	.	.	0.00
6-9m	SPR81	C	5	0.000	0.000	0.00	0.000	0.00
6-9m	SPR81	E	5	0.000	0.000	0.00	0.000	0.00
6-9m	SUM81	C	5	0.000	0.000	0.00	0.000	0.00
6-9m	SUM81	E	5	0.000	0.000	0.00	0.000	0.00
6-9m	SPR82	C	5	0.000	0.000	0.00	0.000	0.00
6-9m	SPR82	E	5	0.000	0.000	0.00	0.000	0.00
6-9m	SUM82	C	10	0.000	0.000	0.00	0.000	0.00
6-9m	SUM82	E	10	0.000	0.000	0.00	0.000	0.00
6-9m	SUM82	Q	5	0.000	0.000	0.00	0.000	0.00

Appendix A, Continued

Species=*SPONGOMORPHA ARCTA*

Depth range	Sample period	T	N	Arithmetic Mean	Mean of log transformed data	Standard error (log_{10})	Geometric Mean	Percent of biomass
0-2m	SUM79	C	5	44.300	1.350	0.34	21.400	1.90
0-2m	SUM79	E	5	18.000	0.970	0.31	8.300	0.80
0-2m	SPR80	C	5	638.800	2.240	0.43	172.800	20.20
0-2m	AUT80	C	4	0.200	0.060	0.06	0.100	0.00
0-2m	AUT80	E	5	10.100	0.820	0.25	5.600	0.40
0-2m	SPR81	E	3	2.100	0.290	0.29	0.900	0.10
0-2m	SUM81	C	5	0.000	0.000	0.00	0.000	0.00
0-2m	SUM81	E	5	0.200	0.060	0.06	0.100	0.00
0-2m	SUM82	C	10	0.000	0.000	0.00	0.000	0.00
0-2m	SUM82	E	10	0.000	0.000	0.00	0.000	0.00
2-3m	SUM79	C	5	0.000	+	0.01	0.000	0.10
2-3m	SUM79	E	5	+	.	.	.	0.00
2-3m	AUT79	C	3	0.000	0.000	0.00	0.000	0.00
2-3m	SPR80	C	5	+	.	.	.	0.00
2-3m	AUT80	E	5	+	.	.	.	0.00
2-3m	SPR81	C	5	0.300	0.100	0.07	0.300	0.20
2-3m	SPR81	E	5	2.400	0.370	0.17	1.300	0.10
2-3m	SUM81	C	5	0.000	0.000	0.00	0.000	0.00
2-3m	SUM81	E	6	0.000	0.000	0.00	0.000	0.00
2-3m	SPR82	C	5	0.000	0.000	0.00	0.000	0.00
2-3m	SPR82	E	6	0.000	0.000	0.00	0.000	0.00
2-3m	SPR82	Q	5	0.000	0.000	0.00	0.000	0.00
2-3m	SUM82	C	10	0.000	0.000	0.00	0.000	0.00
2-3m	SUM82	E	10	0.000	0.000	0.00	0.000	0.00
2-3m	SUM82	Q	5	0.000	0.000	0.00	0.000	0.00
6-9m	SUM79	C	5	+	.	.	.	0.00
6-9m	SUM79	E	5	0.000	0.000	0.00	0.000	0.00
6-9m	AUT79	C	4	0.000	0.000	0.00	0.000	0.00
6-9m	SPR80	C	5	0.000	0.000	0.00	0.000	0.00
6-9m	AUT80	C	5	0.000	0.000	0.00	0.000	0.00
6-9m	AUT80	E	5	0.000	0.000	0.00	0.000	0.00
6-9m	SPR81	C	5	0.000	0.000	0.00	0.000	0.00
6-9m	SPR81	E	5	0.000	+	0.01	0.000	0.00
6-9m	SUM81	C	5	0.000	0.000	0.00	0.000	0.00
6-9m	SUM81	E	5	0.000	0.000	0.00	0.000	0.00
6-9m	SPR82	C	5	0.000	0.000	0.00	0.000	0.00
6-9m	SPR82	E	5	0.000	0.000	0.00	0.000	0.00
6-9m	SUM82	C	10	0.000	0.000	0.00	0.000	0.00
6-9m	SUM82	E	10	0.000	0.000	0.00	0.000	0.00
6-9m	SUM82	Q	5	0.000	0.000	0.00	0.000	0.00

Appendix A, Continued

Species=*ULVARIA OBSCURA*

Depth range	Sample period	T	N	Arithmetic Mean	Mean of log transformed data	Standard error (log_{10})	Geometric Mean	Percent of biomass
0-2m	SUM79	C	5	0.000	0.000	0.00	0.000	0.00
0-2m	SUM79	E	5	0.000	+	0.01	0.000	0.00
0-2m	SPR80	C	5	3.600	0.450	0.21	1.800	0.10
0-2m	AUT80	C	4	0.000	0.000	0.00	0.000	0.00
0-2m	AUT80	E	5	0.000	0.000	0.00	0.000	0.00
0-2m	SPR81	E	3	1.300	0.320	0.14	1.100	0.00
0-2m	SUM81	C	5	0.000	0.000	0.00	0.000	0.00
0-2m	SUM81	E	5	0.000	0.000	0.00	0.000	0.00
0-2m	SUM82	C	10	0.000	0.000	0.00	0.000	0.00
0-2m	SUM82	E	10	0.000	0.000	0.00	0.000	0.00
2-3m	SUM79	C	5	+	.	.	.	0.00
2-3m	SUM79	E	5	0.000	0.000	0.00	0.000	0.00
2-3m	AUT79	C	3	0.000	0.000	0.00	0.000	0.00
2-3m	SPR80	C	5	0.000	0.000	0.00	0.000	0.00
2-3m	AUT80	E	5	0.000	0.000	0.00	0.000	0.00
2-3m	SPR81	C	5	0.000	0.000	0.00	0.000	0.00
2-3m	SPR81	E	5	0.000	0.000	0.00	0.000	0.00
2-3m	SUM81	C	5	0.000	0.000	0.00	0.000	0.00
2-3m	SUM81	E	6	0.000	0.000	0.00	0.000	0.00
2-3m	SPR82	C	5	0.000	0.000	0.00	0.000	0.00
2-3m	SPR82	E	6	0.000	0.000	0.00	0.000	0.00
2-3m	SPR82	Q	5	0.000	0.000	0.00	0.000	0.00
2-3m	SUM82	C	10	0.000	0.000	0.00	0.000	0.00
2-3m	SUM82	E	10	0.000	0.000	0.00	0.000	0.00
2-3m	SUM82	Q	5	0.000	0.000	0.00	0.000	0.00
6-9m	SUM79	C	5	0.000	0.000	0.00	0.000	0.00
6-9m	SUM79	E	5	0.000	0.000	0.00	0.000	0.00
6-9m	AUT79	C	4	0.000	0.000	0.00	0.000	0.00
6-9m	SPR80	C	5	0.000	0.000	0.00	0.000	0.00
6-9m	AUT80	C	5	0.000	0.000	0.00	0.000	0.00
6-9m	AUT80	E	5	+	.	.	.	0.00
6-9m	SPR81	C	5	0.000	0.000	0.00	0.000	0.00
6-9m	SPR81	E	5	0.000	0.000	0.00	0.000	0.00
6-9m	SUM81	C	5	0.000	0.000	0.00	0.000	0.00
6-9m	SUM81	E	5	0.000	0.000	0.00	0.000	0.00
6-9m	SPR82	C	5	0.000	0.000	0.00	0.000	0.00
6-9m	SPR82	E	5	0.000	0.000	0.00	0.000	0.00
6-9m	SUM82	C	10	0.000	0.000	0.00	0.000	0.00
6-9m	SUM82	E	10	0.000	0.000	0.00	0.000	0.00
6-9m	SUM82	Q	5	0.000	0.000	0.00	0.000	0.00

Appendix A, Continued

Species=*UROSPORA WORMSKJOLDII*

Depth range	Sample period	T	N	Arithmetic Mean	Mean of log transformed data	Standard error (log_{10})	Geometric Mean	Percent of biomass
0-2m	SUM79	C	5	0.000	0.000	0.00	0.000	0.00
0-2m	SUM79	E	5	0.000	0.000	0.00	0.000	0.00
0-2m	SPR80	C	5	0.000	0.000	0.00	0.000	0.00
0-2m	AUT80	C	4	0.000	0.000	0.00	0.000	0.00
0-2m	AUT80	E	5	0.000	0.000	0.00	0.000	0.00
0-2m	SPR81	E	3	0.000	0.000	0.00	0.000	0.00
0-2m	SUM81	C	5	0.000	0.000	0.00	0.000	0.00
0-2m	SUM81	E	5	0.000	0.000	0.00	0.000	0.00
0-2m	SUM82	C	10	0.000	0.000	0.00	0.000	0.00
0-2m	SUM82	E	10	0.000	0.000	0.00	0.000	0.00
2-3m	SUM79	C	5	0.000	0.000	0.00	0.000	0.00
2-3m	SUM79	E	5	0.000	0.000	0.00	0.000	0.00
2-3m	AUT79	C	3	0.000	0.000	0.00	0.000	0.00
2-3m	SPR80	C	5	0.000	0.000	0.00	0.000	0.00
2-3m	AUT80	E	5	0.000	0.000	0.00	0.000	0.00
2-3m	SPR81	C	5	0.000	0.000	0.00	0.000	0.00
2-3m	SPR81	E	5	4.700	0.690	0.12	3.900	0.20
2-3m	SUM81	C	5	0.000	0.000	0.00	0.000	0.00
2-3m	SUM81	E	6	0.000	0.000	0.00	0.000	0.00
2-3m	SPR82	C	5	0.000	0.000	0.00	0.000	0.00
2-3m	SPR82	E	6	+	.	.	.	0.00
2-3m	SPR82	Q	5	29.000	1.110	0.34	11.900	2.90
2-3m	SUM82	C	10	0.000	0.000	0.00	0.000	0.00
2-3m	SUM82	E	10	0.000	0.000	0.00	0.000	0.00
2-3m	SUM82	Q	5	0.000	0.000	0.00	0.000	0.00
6-9m	SUM79	C	5	0.000	0.000	0.00	0.000	0.00
6-9m	SUM79	E	5	0.000	0.000	0.00	0.000	0.00
6-9m	AUT79	C	4	0.000	0.000	0.00	0.000	0.00
6-9m	SPR80	C	5	0.000	0.000	0.00	0.000	0.00
6-9m	AUT80	C	5	0.000	0.000	0.00	0.000	0.00
6-9m	AUT80	E	5	0.000	0.000	0.00	0.000	0.00
6-9m	SPR81	C	5	0.000	0.000	0.00	0.000	0.00
6-9m	SPR81	E	5	0.000	0.000	0.00	0.000	0.00
6-9m	SUM81	C	5	0.000	0.000	0.00	0.000	0.00
6-9m	SUM81	E	5	0.000	0.000	0.00	0.000	0.00
6-9m	SPR82	C	5	0.000	0.000	0.00	0.000	0.00
6-9m	SPR82	E	5	0.000	0.000	0.00	0.000	0.00
6-9m	SUM82	C	10	0.000	0.000	0.00	0.000	0.00
6-9m	SUM82	E	10	0.000	0.000	0.00	0.000	0.00
6-9m	SUM82	Q	5	0.000	0.000	0.00	0.000	0.00

Appendix B

A discussion of urchin population size structure

Changes in urchin population structure with depth were similar to those reported for a population sampled from a loose substratum during 1968 at Portugal Cove (Himmelman 1969,1980). Small urchins were uncommon in shallow water, peaked in abundance in the mid to lower barrens, and decreased to lower values in deeper water. Himmelman showed that a similar trend was evident, although less pronounced, on bedrock (Himmelman 1969, 1980), but because air dredge sampling was not employed it is unlikely that small animals were sampled as accurately as those on the loose substratum. Similarly in Nova Scotia (Wharton 1980) and Quebec (Himmelman *et al.* 1983a) small urchins were most abundant in barrens. The low abundance of small urchins in kelp beds in Nova Scotia (Wharton and Mann 1981), and their low abundance within the two depth ranges with abundant fleshy macro-algae at the present site suggests that macro-algae may have a negative influence on urchin recruitment. Pearse *et al.* (1970) hypothesized that large non-calcareous macro-algae reduce urchin recruitment. Tegner and Dayton (1981) noted a negative correlation between recruitment of *Strongylocentrotus franciscanus* and *Macrocystis* abundance in California. This hypothesis is certainly worthy of direct testing, especially since there are other complicating factors (including predation, exposure to wave action, the nature of dominant algae with respect to urchin food preferences, and the nature of the substratum).

There are no obvious trends in growth and mortality evident in the data from 0-2m and 2-3m on the control transect. The population size-structure was

certainly not static, but beyond that little can be said. Detailed analysis of the population structure within the 6-9m samples indicates that growth rates were very low, and interannual recruitment or mortality variations were high. Similarly, Himmelman *et al.* (1983a,b) reported growth rates of 1-1.5 mm y^{-1} for urchins in a barren area in the St. Lawrence estuary. These authors also recorded considerable interannual variation in recruitment, with a heavy recruitment in 1977, followed by no apparent recruitment during 1978-1981. Propp (1977) reported large interannual variations in population structure of *S. droebachiensis*, indicative of fluctuations in recruitment, in the Barents Sea. This pattern is common among herbivorous echinoids (Tegner and Dayton 1981; Andrew and Choat 1982; Ebert 1983), and other benthic invertebrates with pelagic larval phases (Scheltema 1974, Dayton and Tegner 1984).

A striking feature of the urchin population structure at 6-9m was the pronounced mode at 3 mm and the decrease in abundance in the 3 mm to 10 mm range. This is interpreted as evidence of intense predation on small urchins. Martel (1982) reported that urchins occurred in the alimentary tracts of 100% of 38 territorial male cunners (*Tautogolabrus adspersus*) examined from St. Phillips, a typical urchin/coralline habitat 8 km. south of the present study area. Urchins $<$ 5 mm occurred in 14%, between 5 and 10 mm in 100%, and larger than 10 mm in 22 % of the fish examined. Martin (1979) reported urchins in the alimentary tracts of 29% of a random sample of 115 cunners from the same site. Urchins made up 14% of the diet of the total sample by weight. Cunners were the most abundant fish at the study site, often feeding on the benthos in large aggregations of 20-40 individuals (pers. obs.). For example, *Corallina officinalis* supported dense populations of juvenile mussels (*Mytilus edulis* and *Vosella modiolus*), polychaetes, and other invertebrates in the spring when the cunners emerged from their over-wintering sites. Cunners were frequently seen stripping food from *Corallina*, and by late summer the *Corallina* was essentially bare. The effects of cunner foraging in other habitats were less obvious, but may have been equally severe. These data and observations indicate that considerable predation on juvenile urchins by cunners occurs in eastern Newfoundland. The

predominance of urchins in the 5-10 mm size group in the guts of territorial males, the importance of urchins in the general diet of cunners, and the marked decrease in density of urchins beyond 5 mm suggests that size selective mortality occurs due at least in part to predation by cunners.

Another predator, the winter flounder (*Pseudopleuronectes americanus*) was also abundant in the study area, and I have observed that their guts frequently contained urchins in the 5-10 mm range Thus size selective predation on juveniles may be an important factor governing the size structure of the urchin population. Despite high levels of predation enough juveniles survive to maintain the dense adult population, whose grazing maintains the barrens. Andrew and Choat (1982) showed that fish predation on juvenile *Evechinus chloroticus* in New Zealand determined population size-structure, but enough urchins escaped predation to maintain an urchin and coralline dominated habitat.

Propp (1977) reported that juvenile *S. droebachiensis* were most abundant "under a crust of calcareous algae," and in crevices in the Murmansk area of the Barents Sea. Himmelman (1980) made a similar observation for urchins in eastern Newfoundland. At 6-9m the corallines *Lithothamnion glaciale* and *Clathromorphum circumscriptum* occupied 51% cover. These algae were undercut due to the activities of boring animals, and spaces were present underneath. Spaces were also present among the erect parts of *L. glaciale.* Although no quantitative data are available, I have observed that juvenile urchins were most abundant in these holes and spaces. They probably escape predation in these cryptic habitats, and this factor may influence the size frequency distributions. Quantification of these observations, an examination of the size of cryptic portions of the coralline algae in relation to the size of urchins which may occupy them, and a determination of whether mortality or settlement factors are responsible for the distribution of juvenile urchins with respect to coralline algae would be valuable.

Appendix C

Response of molluscan herbivores to urchin removal

Margarites helicinus and *Lacuna vincta* were the only herbivores whose biomass and density were affected by urchin removal. There were increases in recruitment, probably due to increased larval settlement, and survival of *Lacuna*. Survival of *Margarites* was also higher in the presence of the macro-algae which developed following urchin removal. High densities of these species were also observed on small isolated patches of algae in the control area, such as occurred on the tops of some boulders. *Lacuna vincta* is an annual species with a planktonic larval phase (Smith 1973). It appears to settle preferentially in the presence of seaweeds (Smith 1973, Fretter and Manly 1977). These authors also reported a high mortality of *Lacuna* shortly after settlement, as was indicated by the present study. *Lacuna vincta* density increased in Nova Scotia following the decline of urchins, such that *L. vincta* is now the dominant herbivore in newly established kelp beds (Keats pers. obs.; C. Johnson, pers. com.[1]).

Margarites helicinus recruitment also occurred during the late summer and early autumn. Like *L. vincta* it exhibited high early mortality, and is probably an annual species. Unlike *L. vincta*, however, it lacks a planktonic phase (Fretter and Graham 1962). Himmelman *et al.* (1983) also recorded increased densities of *M. helicinus*, but not *L. vincta*, during an urchin removal experiment in Quebec.

The lower mortality of these two species in the presence of abundant

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macroalgae may have been due to increased food availability, and/or reduced effectiveness of predation in the dense algae. The increase in survivorship of *Lacuna* with depth in the presence of macro-algae suggests that wave action may be a significant cause of mortality. Wave stress decreases with increasing depth. Differences in morphology between the dominant *Alaria esculenta* in shallow water, compared with early successional filamentous algae, and later *Desmarestia aculeata* in deeper water may also have influenced the depth dependence of mortality. Depth differences in the abundance of predatory fishes could also produce this pattern, but the distribution of fishes with depth has not been examined in the present study area. The low abundance and patchy distribution of *Margarites* in the shallow macro-algal zone may be a result of wave action and/or a scarcity of filamentous algae upon which egg masses, and newly hatched individuals were most frequently observed. The general biology and ecology of these species in subtidal areas, and factors which influence their recruitment, survival, reproduction and growth are worthy of further study. This is particularly true in view of the potential effect of *Lacuna vincta* on algal populations (Fralick *et al.* 1974; Hooper 1980; Thomas and Page 1983).

The molluscan members of the herbivore guild may have had an impact on community structure. The grazing potential of these herbivores cannot be calculated from available literature, because publications dealing with this phenomenon rarely report herbivore biomass, but rather density. The only molluscan species which has been implicated in large scale effects on macroscopic algae, and which was present in the study area, is *Lacuna vincta.* Fralick *et al.* (1974) reported that a localized population explosion of the species in New Hampshire caused a marked depletion of *Laminaria* spp. Hooper (1980) also reported observing the removal of algal beds by *Lacuna* in Newfoundland. I have also observed mortality of *Laminaria* and other large algae due to browsing by this species in Nova Scotia, Newfoundland, and Labrador. Thomas and Page (1983) reported that following settlement at a density of < 350 m^{-2} during June, *Lacuna vincta* consumed as much as 79% of *Fucus edentatus* net production by August at a site in New Brunswick. This grazing had a major impact on plant

growth and standing crop. *Lacuna* density following settlement at 2-3m on the experimental transect was considerably higher than the mean density recorded by Thomas and Page (1983). Despite this *Lacuna* survivorship was evidently low enough that large scale mortality of macro-algae did not occur. *Alaria* sporelings, however, may have received some grazing damage, and this may have had some limited impact on community composition during the first year after urchin removal. *Margarites helicinus* feeds on diatoms and micro-algae (Fretter and Graham 1962), and presumably spores and germlings of macro-algae. Further details of the diet and feeding abilities of *M. helicinus* are lacking, so its potential impact on macro-algae cannot be assessed.

At a mean density of 70 m^{-2} grazing by *Acmaea testudinalis* has been shown to significantly increase the competitive ability of *Clathromorphum* spp. over other coralline algae (Steneck 1982). Thus at densities observed in the study area *A. testudinalis* may play an important rôle in mediating competition among coralline algae. By grazing spores and sporelings (Willcox 1905) this species could also have direct effects on fleshy algae.

Of the three chiton species present in the study area, *Ischnochiton alba* is probably not a very important grazer, because its abundance was very low. In view of their high densities and biomass both *Tonicella rubra* and *T. marmorea* may have significant effects on macro-algae. Because of the structure and heavy mineralization of the radular teeth, most chitons are capable of excavating coralline algae (Steneck and Wattling 1982). Langer (1978) presented data which suggested that *T. rubra*, *T. marmorea* and *I. albus* are omnivorous species with a strong herbivorous component to their diet. Presumably they may remove micro-algae, spores and germlings of macro-algae, and thereby have the potential to influence community structure. The precise rôle of these abundant herbivores is certainly worthy of study, both in the presence and in the absence of urchins.